ECOLOGICAL RESPONSES TO ALTERED FIRE FREQUENCY IN TREELINE FORESTS OF THE NORTH YUKON, CANADA

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By

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ABSTRACT

Climate change is expected to alter patterns of disturbance, which in turn may drive future ecosystem change. This interaction may be particularly important in sub-arctic regions due to rapid climate change and frequent fire. With increased temperatures in northern ecosystems, there is an assumption that typically southern species will shift their distributions northwards. In the northwestern boreal forest, however, the bottleneck to forest establishment is recruitment, which is strongly mediated by reproductive output and disturbance effects. This research focused on the indirect pathway of disturbance-mediated recruitment. The interaction between fire and forest successional processes in sub-arctic stands undergoing climatic warming was investigated by using field observations and experimental studies at the northern limit of the boreal forest, where the recent fire history created a mosaic of black spruce (*Picea mariana* [Mill.] BSP) stands burned with varying fire return intervals. This research had two main objectives: 1) Identify how fire influences tree recruitment in northern treeline forests, and; 2) Investigate the responses of northern forests to a change in fire return interval. Fire may either accelerate or hinder treeline movement, depending upon regional conditions and fire severity. Recruitment of black spruce was drastically reduced following two closely timed fires (~15 year interval), compared to stands burned under a typical fire return interval, and carbon storage across disturbance intervals was dramatically reduced following short-interval burns. Recruitment was also limited in mature forest stands. On-site germination experiments demonstrated that recruitment was limited by seed availability after a short fire return interval, and by seedbed quality in unburned stands. Once established as seedlings, all native tree species studied benefited from the more favourable environmental conditions for growth in short-interval burned stands. It is predicted that a positive effect of warming, in the form of direct climate effects or

indirect fire effects, on post-fire recruitment potential in the absence of seed limitation. However, this pattern could reverse, becoming a negative effect, if conditions become too dry. Increases in fire activity may thus lead to a degradation of treeline forests in some areas, rather than the increased tree density and forest extent predicted with climate warming.

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LIST OF ABBREVIATIONS

ANCOVA – analysis of covariance

ANOVA – analysis of variance

ARH – adventitious root height

DBH – diameter at breast height (1.47 m)

GLM – generalised linear model

LI – long-interval burn

MANCOVA – multivariate analysis of covariance

MANOVA – multivariate analysis of variance

MF – mature forest

MRPP – multiple response permutation procedure

SE – standard error

SI – short-interval burn

SOC – soil organic carbon

SOH – soil organic horizon

ZANB – zero-altered negative binomial model

ZAP – zero-altered Poisson model

PREFACE

This dissertation is a compilation of four manuscript-style chapters based on data collected and analyzed throughout my degree. The four data chapters are preceded by a general introduction, and are followed by a concluding chapter. Each data chapter is also preceded by a short foreword explaining how the chapter relates to my thesis research.

1.0 INTRODUCTION

1.1 Fire in the boreal forest

Fire is the dominant disturbance initiating secondary succession in the boreal forest of North America, with consequent effects on ecosystem structure and function (Payette, 1992; Weber & Flannigan, 1997). The historic fire regime in these boreal forests consists of stand-replacing fires that occur on a cycle shorter than the lifespan of the dominant tree species (Johnson, 1992). Fire frequency varies widely across different regions of the boreal forest, but in western North America, the interval between fires has historically been 80 to 150 years (Viereck, 1983; Johnson, 1992; Larsen, 1997), by which time individuals have reached reproductive maturity and produced enough seed to self replace after fire (Suffling, 1995).

Tree establishment occurs most rapidly in the first years following fire, when seed availability, seed viability, and seedbed availability are greatest (Johnson & Fryer, 1989; Johnstone *et al.*, 2004). Soil temperature and moisture, soil organic horizon (SOH) thickness, and understory competition all contribute to the ability of a seed to germinate and survive in a given location (Eriksson & Ehrlen, 1992; Greene *et al.*, 1999). Generally, a newly established seedling requires a consistent source of moisture, suitable temperatures for growth and survival, and access to sunlight. Optimal seedbed conditions that are typically present immediately after fire deteriorate rapidly in the first few years after fire (Charron & Greene, 2002; Peters *et al.*, 2005). Although all tree species characteristic of the boreal forest do not have the same seedbed requirements, generally their establishment is negatively correlated with SOH thickness (Purdy *et al.*, 2002; Johnstone & Chapin, 2006a; Hesketh *et al.*, 2009). Organic horizons, which are dominated by moss and lichens in the boreal forest, are very poor seedbeds due to the increased drought stress caused by the porous organic surface. This is particularly important for small

seeded, deciduous germinants, which are very sensitive to desiccation (Johnstone & Chapin, 2006a; Greene *et al.*, 2007).

The short recruitment window the occurs in the first few years after fire means that fire-initiated boreal forest stands are generally evenly aged (Payette, 1992). Seedbed condition is a very important driver of stand-age structure in boreal forests. In northern boreal forest stands, fires are generally of low severity, meaning that organic horizons are often only partially combusted (Greene *et al.*, 2007). The resulting seedbed has a dark, charred surface that can be prone to desiccation, killing young seedlings (Johnstone & Chapin, 2006a). Boreal tree species demonstrate a variety of adaptations for regeneration that allow them to establish under these conditions, including aerial seed banks of serotinous cones in some conifers and vegetative re-sprouting of deciduous species from roots and stumps following fire (Zasada *et al.*, 1992; Li, 2000). The regeneration strategy of serotiny allows for a pulse of regeneration following fire as the heat-opened cones release multiple years' production of seed (Lamont *et al.*, 1991; Lamont & Enright, 2000). The large number of seeds that black spruce release after fire helps ensure that, despite potentially unfavourable seedbed conditions in some patches, enough black spruce disperse to favourable microsites to facilitate post-fire stand self-replacement (Viereck, 1983; Johnstone *et al.*, 2010a). As time passes after fire, moss and lichen communities establish and recover to the point that the seedbed becomes unfavourable and tree recruitment decreases dramatically. This interaction between post-fire seedbed condition and regeneration strategy may stabilize successional cycles in boreal forest stands, maintaining ecological resilience (Johnstone *et al.*, 2010a).

Fire is also the dominant disturbance affecting net ecosystem productivity in the boreal forest of North America (Bond-Lamberty *et al.*, 2007; Jonsson & Wardle, 2010). The

circumboreal forest contains more than one-third of the world's carbon stored in terrestrial ecosystems (Kasischke, 2000; McGuire *et al.*, 2002; Tarnocai *et al.*, 2009). Following fire, the boreal forest shifts from acting as a carbon sink to a source of carbon for several decades, as the rate of above- and below-ground decomposition exceeds photosynthesis and growth (Amiro *et al.*, 2003; Chapin *et al.*, 2006; Kashian *et al.*, 2006). As the forest regenerates, it returns to acting as a carbon sink, sequestering carbon in soil, vegetation, and dead wood. Under stable disturbance conditions, net ecosystem productivity remains stable or may slightly increase across disturbance intervals (Harden *et al.*, 2000; Bond-Lamberty *et al.*, 2007).

1.2 Climate change and the fire regime

The Earth has entered a period of rapid climate change, particularly in the past half century (Millennium Ecosystem Assessment, 2005). Global climate warmed approximately 0.6 ± 0.2 ^{o}C in the 20th century (Houghton *et al.*, 2001). The increase in temperature is not uniform, however, and the effects of climate change are predicted to be greatest in arctic and sub-arctic regions (ACIA, 2004). Climate warming is already occurring faster in the circumpolar north than temperate regions (Solomon *et al.*, 2007). The highest air temperatures in the arctic during the past 400 years occurred in the 20th and 21st centuries (Overpeck *et al.*, 1997; Serreze *et al.*, 2000; Shulski & Wendler, 2007). In sub-arctic regions of northwestern North America, summer air temperature increased by 2^{o} C between 1961 and 2004 (Chapin *et al.*, 2005).

Climate change will impact ecosystems via direct temperature effects and indirect effects caused by changes to disturbance regimes. Boreal forests established in northwestern North America during the mid-Holocene (approximately 7000 years ago) and have maintained a relatively stable composition and extent in that region for the past five or six millennia, following the arrival of black spruce (*Picea mariana* [Mill.] B.S.P.; Lynch *et al.*, 2004; Lloyd *et al.*, 2006;

Chapin *et al.*, 2010). Climate was a major driver of the establishment and maintenance of boreal forests in this region; for example, black spruce expansion in the region occurred after a shift to cooler, higher moisture conditions (Lloyd *et al.*, 2006). It is not yet clear how fire interacted with climate and vegetation during the Holocene, however there is evidence that fire return intervals fluctuated from >500 to 150 years (Lynch *et al.*, 2004). Paleoecological evidence indicates that climate and vegetation controls over the fire regime were not equivalent for the entirety of the boreal forest, but instead varied regionally (Lloyd *et al.*, 2006). Paleoecological studies suggest that changes in fire regime during the Holocene were driven by vegetation change in Alaska (Lloyd *et al.*, 2006; Higuera *et al.*, 2009) compared to climate in eastern Canada (Carcaillet *et al.*, 2001; Lloyd *et al.*, 2006). These findings emphasize the importance of understanding local and regional controls over vegetation-fire dynamics for predicting future forest composition and disturbance regimes.

Fire patterns in the boreal forest, such as fire size and severity, are largely driven by weather and local moisture conditions (Renkin & Despain, 1992; Bessie & Johnson, 1995; Podur & Martell, 2009). In the boreal forest of North America, warming summer air temperatures increase the susceptibility of an area to burn in a wildfire (Wagner, 1987; Lee, 1995; Skinner *et al.*, 2002). With increased warming, several aspects of the fire regime are predicted to change including an increase in, for example, fire frequency, total burned area, length of the fire season, and fire severity (Weber & Flannigan, 1997; Kasischke & Turetsky, 2006; Flannigan *et al.*, 2009). Increases in fire frequency and area burned have already being observed in some regions (Gillett *et al.*, 2004; Kasischke & Turetsky, 2006; Flannigan *et al.*, 2009). There is uncertainty associated with these predictions (Flannigan *et al.*, 2009), however, such as the extent to which these changes to the fire regime will occur in different regions of the boreal forest. Multiple

studies indicate that changes to fire weather, or the conditions that contribute to the probability of a fire occurring, vary spatially due to the complex interactions between climate, vegetation, and human activity (see Flannigan *et al.*, 2009). The predicted interaction between climate warming and the fire regime have the potential to overshadow any direct effects of climate on boreal forest composition and distribution (Weber & Flannigan, 1997). Understanding the impacts of a changing fire regime is thus critical to predicting future changes in boreal forest cover.

1.3 Fire-climate interactions in the sub-arctic

The latitudinal treeline is a distinctive feature of sub-arctic North America (Timoney *et al.*, 1992). The treeline is an ecotone: the transition from the northern extent of the boreal forest to the sub-arctic tundra. Ecotones may be used for the early detection of climate change (e.g., Solomon, 1986; Grace *et al.*, 2002; Korner & Paulsen, 2004). Treelines are predicted to undergo significant structural and positional changes with climate change in the arctic (Grace *et al.*, 2002) as environmental constraints on tree establishment lessen with warming in northern regions. Tree species at the limit of their range are sensitive to variability in climate because of the abiotic factors that dominate the control over their establishment (Brubaker, 1986; Noble, 1993; Germino *et al.*, 2002; Holtmeier & Broll, 2005; Macdonald *et al.*, 1998). Northern treeline advance has already been documented in latitudinal and altitudinal treelines globally (e.g., Gamache & Payette, 2005; Truong *et al.*, 2006; Harsch *et al.*, 2009), however, recession of treelines has also been associated with disturbance in some areas (Payette *et al.*, 1989; Payette *et al.*, 2001; Speed *et al.*, 2011).

If fire activity increases in association with warming summer temperatures in northern boreal ecosystems (Kasischke *et al.*, 1995; Chapin *et al.*, 2005; Kasischke & Turetsky, 2006; Balshi *et al.*, 2009; Flannigan *et al.*, 2009), this may have a strong impact on both forest cover

and treeline dynamics. Here, I define northern boreal forests as coniferous-dominated forests underlain by continuous or discontinuous permafrost, and include in this category the treeline regions of the sub-arctic. Previous research has suggested that reductions in the fire cycle can cause reduced seed production (Black & Bliss, 1980), reduced recruitment of conifers, and increased deciduous recruitment in northern boreal stands (Landhausser & Wein, 1993; Johnstone & Chapin, 2006b). Additional research is needed to understand how climate and fire may interact to affect forest cover at the northern limits of the boreal forest, where direct climate effects on regeneration are likely to be strongest. It is possible that the indirect effects of climate on forests via a change in the disturbance regime could lead to a net effect on forest composition that may be very different from what would be predicted from the direct effects of climate alone.

The consequences of changing disturbance regimes for ecosystems and communities are a priority for global change research (Turner, 2010). We do not yet know how these processes will interact to shape sub-arctic ecosystems. In particular, we do not know how the indirect effects of climate on the disturbance regime will influence the structure and composition of northern forest stands that have adapted to historic fire regimes. These indirect effects may potentially cause responses that are stronger and in the opposite direction to the expected direct effects. Climate-driven changes to fire severity or frequency may cause shifts in forest composition or structure (Greene & Johnson, 1999; Johnstone & Chapin, 2006b; Westerling *et al.*, 2011), which will have a significant impact on ecosystem functions including albedo, carbon storage, and subsequent disturbance regimes (Chapin *et al.*, 2000; Eugster *et al.*, 2000; Grace *et al.*, 2002; Chapin *et al.*, 2005; McGuire *et al.*, 2006).

The goal of the research presented in this thesis was to investigate the interaction between fire and forest successional processes in sub-arctic black spruce stands undergoing climatic

warming (Figure 1-1). This was done using field observations and experimental studies at the northern limit of the boreal forest, where the recent fire history created a mosaic of stands burned with varying fire return intervals. These overlapping fires were used as a natural experiment to examine the impacts of fire return interval on ecosystem structure and function. Natural experiments such as this one are inherently confounded with other spatial gradients due to the patchy, landscape process of burning. However, experimental manipulations of landscape-scale fires is not feasible and natural experiments like the one presented here provide vital empirical data on the potential impacts of altered fire regimes (Turner *et al.* 1997; Turner, 2010).

This thesis summarizes the results of these field observations and experimentation. In Chapter 2, I investigated the reproductive capacity of northern forest stands across the treeline ecotone. I hypothesized that the reproductive output of individual trees would be lower at the margin of tree occurrence than within continuous boreal forest. In that situation, near-treeline forest stands may play a key role as a seed source for treeline expansion. Thus the dynamics of adjacent northern forests may act as important controls over the potential for expansion or retraction of the local treeline. In Chapter 3, I investigated how an altered fire return interval can interrupt successional pathways by altering the regeneration potential of these northern forests (Figure 1-1). My study area in the northern black spruce forest represents one of several types of serotinous ecosystems in the circumboreal biome (Zasada *et al.*, 1992), where the dominant canopy species rely on an aerial seedbank for post-fire regeneration (Johnson, 1992; Payette, 1992). I hypothesized that black spruce recovery in stands experiencing a short fire return interval would be severely reduced due to the lack of an aerial seed bank produced by the local, immature trees. By affecting seed availability, changes in fire activity caused by climate change

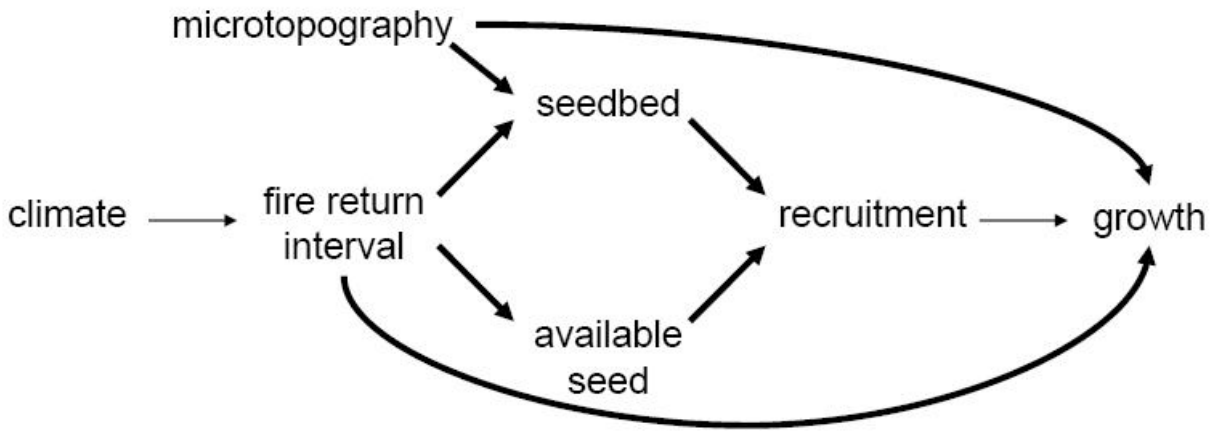

Figure 1-1: A conceptual diagram of fire, vegetation, and climate relationships driving secondary succession in the boreal forest. Relationships investigated in this thesis are connected by a bold arrow.

could influence the regeneration potential of this dominant forest type. In Chapter 4, I compared seedling establishment and growth of black spruce, white spruce (*Picea glauca* (Moench) Voss), Alaskan birch (*Betula neoalaskana* Sarg.), balsam poplar (*Populus balsamifera* L.), and trembling aspen (*Populus tremuloides* Michx.) in stands of varying fire return interval using an experimental manipulation overlaid on the natural treatment contrasts created by the fire history mosaic of the study area. I hypothesized that black spruce seedbed quality would be highest in stands that were exposed to a typical, long fire return interval of the northwestern boreal forest, whereas seedbed composition in a frequently burned stand would provide a more suitable seedbed for upland tree species, due in part to warmer and drier soils. I hypothesized that mature forest stands, which had a well developed forest floor, would provide an unsuitable seedbed for all species examined and poor environmental conditions for planted seedling growth. Investigation of these substrate effects on the recruitment and growth of canopy tree species provides insights into the indirect pathways by which fire history may shape forest dynamics even when seed is not limiting (Figure 1-1). Finally, in Chapter 5, I quantified and compared the amount of carbon consumed during, and remaining following, fire in black spruce forests burned after long- vs. short-intervals, testing the hypothesis that a shortened fire return interval would result in greater consumption of carbon from black spruce forest stands than those that have experienced a typical fire return interval. This research provides a context for exploring the effects of changes in fire regime on a globally-relevant ecosystem service of boreal forests, namely carbon storage. Together, these chapters provide a case study of the reproductive and environmental consequences of a change in fire history for northern black spruce forests. The results provide much-needed empirical evidence of how climate-driven changes in fire regime may shape the dynamics of boreal forests in a coming century of rapid environmental change.

2.0 REPRODUCTIVE POTENTIAL OF BLACK SPRUCE ACROSS THE NORTHERN BOREAL TREELINE ECOTONE

FOREWORD

This chapter summarizes an observational study of the structure and reproductive capacity of black spruce stands across the treeline ecotone in northern Yukon. The results presented here provide context for the subsequent experimental work presented in this thesis by highlighting the importance of northern boreal forests for regeneration at treeline. This chapter represents one component of an International Polar Year synthesis manuscript on reproductive capacity across the circumpolar treeline ecotone, which I am preparing for submission to the journal Ecography.

2.1 INTRODUCTION

The arctic is undergoing a trend of climatic warming (Chapin *et al.*, 2005), but the repercussions of this warming on ecosystems and related processes have yet to be definitively identified (Euskirchen *et al.*, 2009; Chapin *et al.*, 2010; Euskirchen *et al.*, 2010). In the northern forest-tundra ecotone, environmental conditions (e.g., summer temperature) have a stronger control on treeline position than biotic interactions (e.g., competition; Holtmeier & Broll, 2005). Unfavourable environmental conditions, such as low air and soil temperatures, limit tree growth and reproduction (Körner, 1998; Sveinbjörnsson *et al.*, 2002; Harsch & Bader, 2011). These unfavourable conditions may directly or indirectly contribute to treeline position via: 1) stress, such as repeated damage or tree growth impairment by frost; 2) disturbance, such as mechanical damage or removal of biomass by wind or herbivory; 3) constraints on reproduction caused by, e.g., reduced pollination, seed development, seedling establishment; 4) carbon balance, where there may be insufficient carbon acquisition for seedling maintenance and growth; and 5) growth limitation by insufficient sugar and protein synthesis by plants (see Körner (1998) and references therein).

As climate warms, it is anticipated that some species will expand their ranges northwards (and upwards, in alpine ecosystems) as environmental constraints on establishment lessen. Summer air temperatures are increasing in the sub-arctic (Chapin *et al.*, 2005), which should lessen environmental constraints on the northern distribution of the boreal forest. Treelines are predicted to undergo significant structural and positional changes with climate change in the arctic (Grace *et al.*, 2002). For example, the boreal forest is expected to move northward as the climate warms, expanding into tundra ecosystems (Kaplan *et al.*, 2003; Holtmeier & Broll, 2005), although recent observations have documented both expansion, stand infilling, and range

retraction at sub-arctic and alpine treeline sites with warming temperatures (Harsch *et al.*, 2009; Harper *et al.*, 2011).

Modelling and experimental evidence have shown a time lag between a period of climatic warming and a shift in treeline vegetation (Chapin & Starfield, 1997; Macdonald *et al.*, 1998; Lloyd & Fastie, 2003; Lloyd, 2005). One of the leading explanations for this time lag is seed limitation, caused by a low productivity or poor dispersal of seeds (Masek, 2001; Walther *et al.*, 2005). While some tree species are quite successful at vegetative reproduction, most trees of boreal treeline need to reproduce sexually to expand at the landscape scale. Sexual reproduction varies from year to year, and is influenced by factors related to pollination, fertilization, and climate (Sirois, 2000). Variability in seed production means that years with favourable climate may drive increased seed production.

Black spruce is a dominant species in the boreal forest of North America, and an important species in the latitudinal treeline of Canada and Alaska (Black & Bliss, 1980; McLeod & Macdonald, 1997). Black spruce is able to survive in these northern climes due to its tolerance of cold, wet soils (Black & Bliss, 1980). As with other species, vertical growth and production of cones by black spruce are limited at the northern margin of its range (Black & Bliss, 1980; Sirois, 2000).

The objective of this study was to quantify the reproductive potential of black spruce across the treeline ecotone, from northern continuous forest to treed tundra. I hypothesized that seed production and viability would decrease with forest density and would be variable from year to year. I tested these hypotheses by measuring black spruce seed production and viability across the treeline ecotone during three growing seasons. This study examined an important gap in our knowledge regarding the reproductive potential of treeline forests for expansion in a

changing climate. Here, I provide empirical evidence of the reproductive capacity for treeline expansion and infilling in a region of sub-arctic Canada currently experiencing climatic warming (Chapin *et al.*, 2005).

2.2 METHODS

2.2.1 Study area description

This study was conducted in treeline forests in the Eagle Plains region of Yukon Territory, Canada (66°06'56"N, 137°16'11"W). The region is composed of unglaciated, rolling topography dominated by fine grain loess soils over weathered bedrock (Smith *et al.*, 2004). These Turbic Cryosols, underlain by continuous permafrost, form a patterned microtopography of earth hummocks (Smith *et al.*, 2004) that create an important moisture, temperature, and instability constraint on soil characteristics in the area. Eagle Plains has a continental climate. The nearest weather stations, in Dawson City (~290 km SW; 64°02'35"N, 139°07'40"W) and Old Crow (~190 km NW; 67°34'14"N, 139°50'21"W) YT, have mean annual air temperatures of -4.4°C and -9°C, and monthly mean temperatures of -26.7°C and -31.1°C in January, and 15.6°C and 14.6°C in July (Environment Canada, 2011). The mean annual precipitation is 324 mm in Dawson City and 266 in Old Crow, about half of which falls as rain in the summer in both locations (Environment Canada, 2011).

The study area was dominated by black spruce with an understory of evergreen shrubs, willows (*Salix* spp.), and *Sphagnum* and feather mosses (e.g., *Hylocomium* spp.; Russell *et al.*, 1992). Black spruce trees produce their seed in semi-serotinous cones that are maintained over consecutive years in an aerial seed bank (Zasada *et al.*, 1992). The cones develop from buds initiated during the previous growing season. The semi-serotinous reproductive strategy of black spruce means that individuals maintain at least three years of cone production at any given time.

These annual cohorts of cones are distinguishable by cone colour and position on the tree. Because the cones are not completely serotinous, they open with age and heat. The oldest cohorts of cones on a black spruce are partially or completely open and have released a portion of their seed (Zasada *et al.*, 1992; Greene *et al.*, 1999).

2.2.2 Field methods

Study sites were established across a gradient from closed black spruce forest to treed tundra (Figure 2-1). Four density zones of black spruce forest were sampled along a north-south gradient: forest, transitional forest, open forest, and treed tundra (Table 2-1). Zones were classified by visual estimation of stand density and basal area. Sampling in each forest zone took place along a 100 m north-south transect. The starting point of each transect was determined by first identifying an area in each forest zone adjacent to the Dempster Highway. Transect starting points were positioned a minimum of 80 m from the highway to avoid the effects the road may have on environmental conditions (Auerbach *et al.*, 1997).

Mature black spruce cones were collected from 10 randomly selected trees along each transect in August 2007, 2008, and 2009. I selected individuals by using a random number generator to determine the number of paces to travel along the north-south transect between sample trees. This method reduced the likelihood of selecting the same tree for sampling in multiple years. Ten mature cones from the current year's cohort were collected from each tree, sampled from branches around the entire circumference of the tree. Cones were identified as mature once they were resin-sealed and predominantly light brown in colour, in comparison to immature, purple cones. Grey and partially opened cones were identified as over-mature and were avoided. I conducted exact counts of all cones, regardless of cohort, present on individuals sampled in 2008 and 2009.

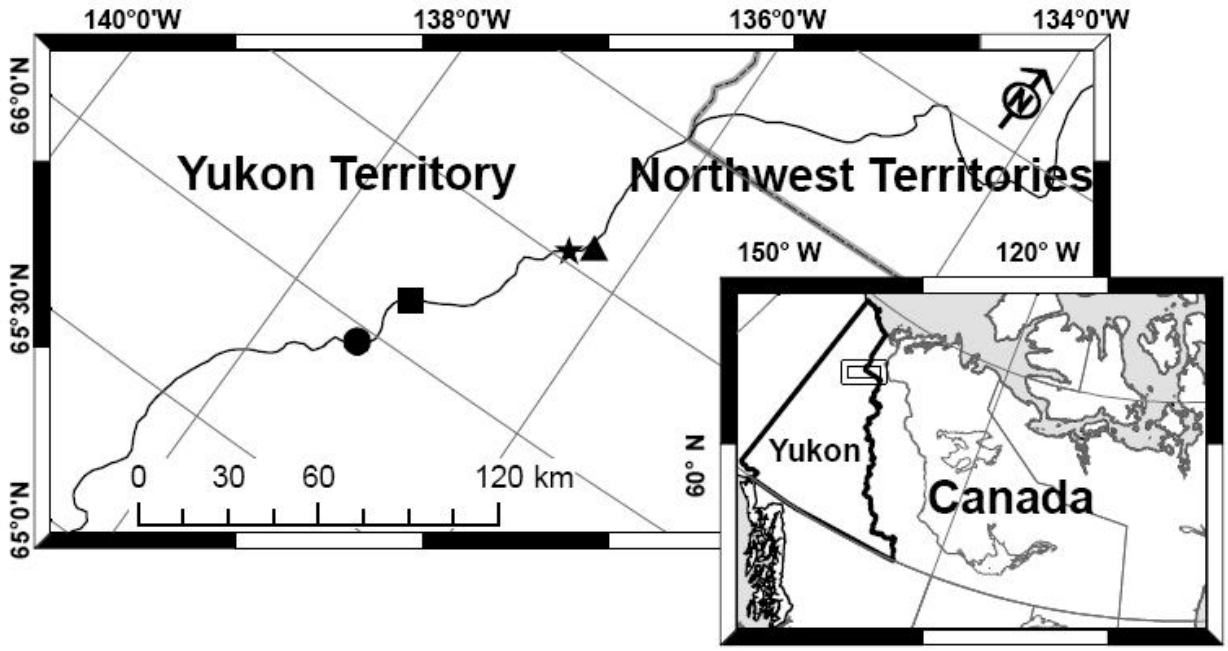

Figure 2-1: Location of study area in northern Yukon. Four forest zones were examined: forest (circle), transitional forest (square), open forest (star), and treed tundra (triangle). Three sampling sites were located within each forest zone.

Table A: Characteristics of forest zones across treeline. Values are means (SE) calculated from samples in each zone (n=10).

Forest zone	SOH thickness (cm)	Depth of thaw (cm)	Oldest tree (years)
Forest	12.2 (1.8)	38 (6)	126
Transitional forest	11.4 (1.7)	34 (3)	181
Open forest	5.8 (1.9)	45 (6)	155
Treed tundra	7.3 (2.4)	48 (6)	110

Soil organic horizon (SOH) thickness and depth of thaw were measured at nine points in association with each transect. Measurements were taken at 0, 50, and 100 m distances along the transect as well as at points 50 m to the east and west of each distance. Measurements occurred at one earth hummock and in one hollow at each of the nine points, for a total of 18 measurements of each variable per site. I excavated 10 cm x 10 cm samples of SOH, from forest floor to mineral soil surface, during the summer of 2007. The thickness of each organic horizon was measured, and then averaged to obtain a mean value for hummocks and hollows in each site. Depth of thaw was measured by inserting a stainless steel probe into the ground until it made contact with permafrost. These measurements were taken during the second week of August, 2007 to capture the deepest thaw possible during field season. At each of the nine points, four black spruce trees were sectioned or cored at ground level for age determination. The nearest individual in each cardinal direction was sampled.

2.2.3 Laboratory analysis and germination trials

Cones were stored frozen until seeds were extracted. After thawing, cones were soaked in warm water for 24 hours and then spread out to air dry for 24 to 72 hours. Samples were then baked in a drying oven for 16 hours at 60°C and allowed to cool to room temperature. Cone samples were agitated by hand in a closed container for several minutes, after which the samples were sieved to separate black spruce seed from the cones and debris (seed extraction protocol from S. Green, personal communication). This seed extraction process, from soaking to sieving, was repeated three times per sample to remove all of the seed from the semi-serotinous cones. Seeds were stored frozen at -16°C until germination trials were initiated.

I assessed the viability of black spruce seeds using laboratory germination trials each winter following the summer field collection of cones. I pooled each year's cone samples by tree

for seed extraction and germination trials, except in 2008 when seed was tested at the individual cone level. I counted the total number of seeds in each sample. The seeds from each sample (trees in 2007 and 2009, individual cones in 2008) were tested in a single 100x15 mm Petri dish, except where samples had more than 100 seeds and were divided into multiple dishes. Seeds were allowed to germinate for 28 days at 18 hours of light per day at room temperature (~20°C), watered with deionised water. Seeds were considered germinated when their hypocotyl grew to twice the length of the seed coat (Leadem *et al.*, 1997). The total number of seeds, number of germinated seeds, and proportion of viable seed were calculated for each sample.

I considered the number of seeds that germinated as the minimum number of viable seeds present in the sample. Although not all viable seeds may have germinated, this method allowed for the measurement of the germination of non-dormant individuals. I assumed that individuals that did not germinate would also be unavailable for recruitment under field conditions due to dormancy or an underdeveloped or absent embryo. Dissection of ungerminated seeds from the 2007 sample revealed that a low proportion of ungerminated seeds contained an embryo (forest: 0.16±0.02; transitional forest: 0.09±0.02; treed tundra: 0.07±0.02). Dormancy of black spruce seeds is low or absent in populations in Saskatchewan (Qualtiere, 2008) and Alaska (Densmore, 1979).

Tree sections were prepared for aging by using a band saw to create a level surface and sanding with progressively finer sandpaper, up to 400 grit. Sections were scanned and aged using WinDENDRO 2008 software (Régent Instruments, Québec, QC). Ring counts were made along two radii on each stem section, from pith to bark. The radius with the greatest number of rings was taken as the minimum age of the stem. The oldest sample from each forest zone was designated as minimum stand age.

2.2.4 Statistical analyses

I first used multivariate analysis to test whether forest structure, as represented by forest density and basal area, differed between forest zones. The data did not meet the assumptions of homogeneity of variance and normality typically required for parametric tests (Scheiner, 1993). As an alternative, I used a multiple response permutation procedure (MRPP), which provided a nonparametric test of differences between two or more groups of sampling units by using repeated shufflings of the distance matrix (Mielke, 1984; McCune & Grace, 2002; Mielke & Berry, 2007). MRPP calculates chance-corrected within-group agreement, which is a descriptor of within-group homogeneity, compared to the random expectation (McCune & Grace, 2002). I conducted the MRPP calculated with Euclidean distances between sample plots (Zimmerman *et al.*, 1985) and groups defined by forest zone (n=3 per zone). The results of MRPP can be interpreted in a similar manner to ANOVA, where a significant p-value indicates a detectable difference between group means. The null hypothesis is that there is no difference between within-group and between-group distance. MRPP analysis results in the calculation of a test statistic, *t*, and within-group agreement value, A.

I first analyzed the proportion of seeds germinated using a generalised linear model (GLM) with a binomial error structure and logit link (Crawley, 2005) with forest zone (forest, transitional forest, open forest, and treed tundra) and year (2007-9) as response variables. The resulting model had a residual scaled deviance that was 17.5 times larger than the residual degrees of freedom indicating overdispersion, or additional unexplained variance in the response variable (Crawley, 2005). I refit the model using quasi-binomial error structure to account for this overdispersion. The quasi-binomial error structure adds an empirical scale parameter to the variance, calculated by dividing the Pearson chi-square by the degrees of freedom (Crawley, 2007). The scale parameter helps to account for the errors being larger than the binomial error

that we assumed in the first model (see Achigan-Dako *et al.*, 2009; Le Roux *et al.*, 2010; and Schoeman *et al.*, 2010 for other examples of studies using this approach).

Seed production in each forest zone was estimated by a suite of related variables: the proportion of seed germinated, number of seeds per cone, number of seeds per tree (seeds per cone x cones per tree), number of germinated seeds per tree (seeds per tree x proportion germinated), number of seeds per hectare (seeds per tree x trees per hectare), and number of germinated seeds per hectare (seeds per hectare x proportion germinated). I used these as multiple response variables representing the reproductive potential of each forest zone. Since the data did not meet the assumptions of homogeneity of variance and normality for parametric tests, I tested for differences between forest zones using MRPP calculated with Euclidean distances between sample plots (n=30 per forest zone).

The number of seeds per cone and proportion of viable seeds per cone measured in 2008 were analyzed using GLMs with quasi-Poisson and quasi-binomial error structures (Crawley, 2007), respectively. I tested for differences in individual trees within each forest zone. The number of cones per tree counted in 2008 and 2009 were also compared using a GLM with quasi-Poisson error structure with forest zone and year as predictor variables.

Depth of thaw and SOH thickness were analyzed as a multiple response using multivariate analysis of variance (MANOVA) forest zone and microtopography (hummock and hollow) as predictor variables. As with ANOVA, MANOVA tests for significant differences between group means, based on categorical predictor variables. MANOVA is used when more than one response variable has been measured (Scheiner, 1993). Here, I conduct MANOVA using Pillai's Trace test statistic (Scheiner, 1993). Pillai's Trace tests the null hypothesis that the group means of the response variables are equal. Two-way ANOVAs were run on each response

variable following a significant MANOVA. To increase the comparability with the other analyses conducted, I also analysed the multiple responses using two separate MRPP analyses: one with groups defined by forest zone, and the other by microtopography. I explored the relationship between SOH thickness and depth of thaw using Pearson's product-moment correlation (Crawley, 2007).

For all models, I assessed model fit using residual diagnostics (Zuur *et al.*, 2009). All statistical analyses, except MRPP, were conducted with R (R Development Core Team, 2009) using the "MASS" package for negative binomial GLMs (Venables & Ripley, 2002). MRPP was performed using PC-ORD version 4 (McCune & Mefford, 1999).

2.3 RESULTS

2.3.1 Patterns in reproduction across the treeline

As per the definition of treeline, forest density and basal area generally decreased from forest to treed tundra (Figure 2-2; Table 2-1). Treed tundra had slightly higher stand density than open forest stands, however an ANOVA of tree height within each forest zone indicated that vertical growth was significantly reduced in treed tundra ($F_{3,132}$=63.36, p<0.0001). Forest structure differed significantly between forest zones (MRPP chance-corrected within-group agreement = 0.417, t = -3.43, p=0.004). Between-plot variance was largest within the forest group (average distance = 713.4) and was lower within the forest transition (average distance = 153.7), open forest (average distance = 4.61), and treed tundra groups (average distance = 39.6), indicating an overall decrease in heterogeneity of forest structure from forest to treed tundra stands. Treed tundra stands had more heterogeneous forest structure than open forest stands, but were still less heterogeneous than transitional forest stands.

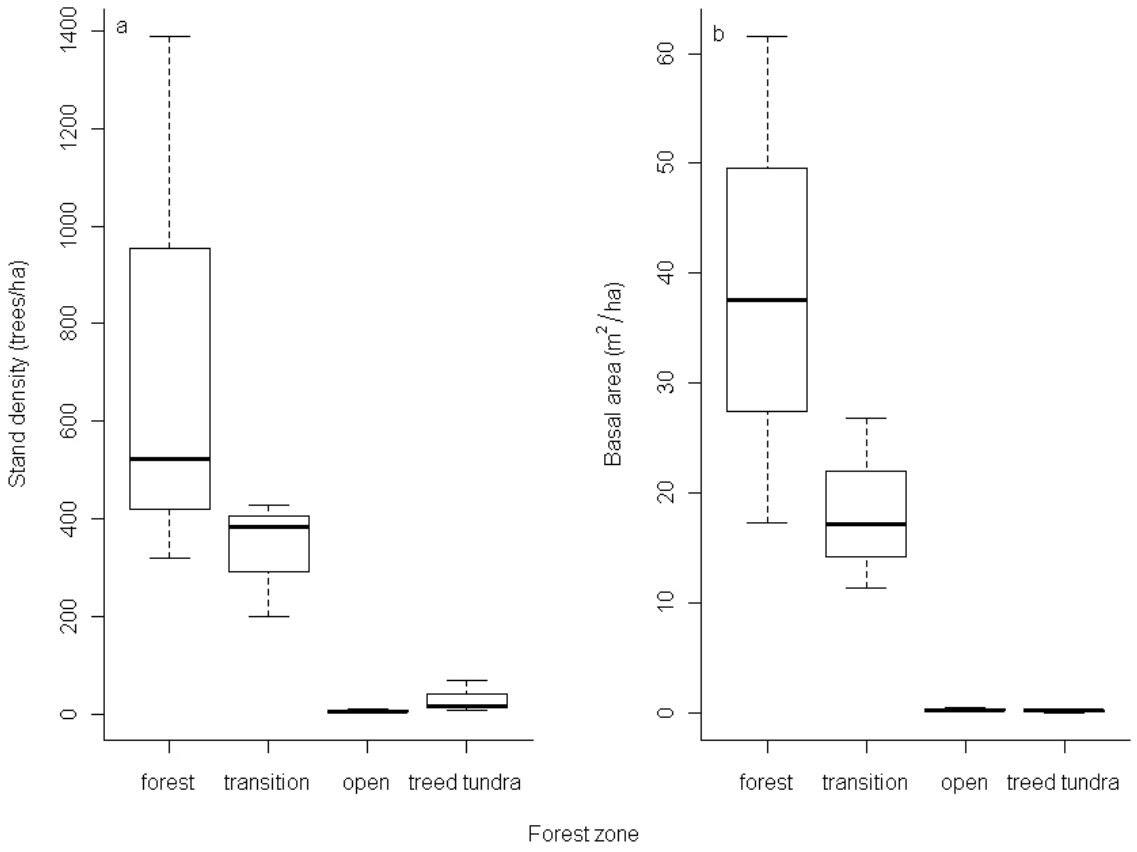

Figure 2-2: Forest density (a) and basal area (b) in forest, transitional forest (transition), open forest (open), and treed tundra sites across the treeline ecotone in northern Yukon (n=3 sites/zone). Boxes encompass the 25%-75% quartiles of the data, with the median indicated by the line through the centre of the box. Whiskers extending from the box encompass the 95% quartiles.

The GLM with quasi-binomial error structure detected a significant interaction between zone and year, where the proportion of seeds that germinated from open forest and treed tundra sites were particularly low in 2008. Overall, the proportion of seed that germinated did not differ between zones, but did vary between years sampled (Figure 2-3, Tables 2-2 and 2-3). A significantly lower proportion of seeds germinated in 2009 than in 2007 or 2008.

Reproductive potential differed significantly between forest zones (MRPP chance-corrected within-group agreement = 0.433, t = -33.8, and $p<0.0001$). The number of seeds per cone (Table 2-2), number of seeds and germinated seeds per tree (Figures 2-4a and b), and number of seeds and germinated seeds per hectare (Figures 2-4c and d) generally decreased across the treeline transition, from forest to treed tundra. Treed tundra had marginally more germinated seeds per tree than open forest stands (Figure 2-4b). As with forest structure, between-plot variance was largest within the forest group (average distance = 19.6×10^5) and was lower within the forest transition (average distance = 9.9×10^5), open forest (average distance = 0.2×10^5), and treed tundra groups (average distance = 0.4×10^5). This difference in between-plot variance indicates that heterogeneity of the reproductive variables was lower closer to treeline. Between-plot variance was greater in treed tundra than open forest stands, potentially driven by the forest structure component of the multivariate response variable.

Cone-level seed production varied between cones on individual trees sampled in 2008, where some trees produced significantly more seeds per cone than others within the same zone. Number of seeds per cone ranged from 0-60 seeds/cone in forested stands (mean=19 ± 2 seeds/cone), 0-71 seeds/cone in transitional forest stands (mean=31 ± 2 seeds/cone), 0-85 seeds/cone in treed tundra (mean=32 ± 2 seeds/cone), and 0-58 seeds/cone in treed tundra

Table B: Reproductive patterns involving black spruce seed across treeline (mean with standard error in parentheses).

	Year	Forest	Transitional forest	Open forest	Treed tundra
Seeds per cone	2007	8.0 (1.5)	4.8 (1.2)	2.2 (0.6)	2.8 (1.0)
	2008	18.7 (1.9)	31.4 (2.7)	32.4 (3.1)	20.0 (2.0)
	2009	36.1 (4.4)	38.3 (4.5)	11.7 (3.2)	10.6 (2.5)
Seeds per tree	2007	1269 (231)	664 (163)	444 (127)	295 (101)
	2008	2948 (296)	4335 (377)	6488 (623)	2112 (207)
	2009	5707 (691)	5280 (626)	2338 (637)	1119 (263)
Seeds per ha ($x10^4$)	2007	94.36 (17.18)	22.40 (5.52)	0.29 (0.08)	0.93 (0.32)
	2008	219.26 (21.99)	146.29 (12.74)	4.28 (0.41)	6.63 (0.65)
	2009	424.43 (51.38)	178.20 (21.14)	1.54 (0.42)	3.51 (0.83)
Viable seeds per tree	2007	334 (78)	260 (71)	70 (25)	72 (23)
	2008	599 (93)	1161 (297)	110 (80)	53 (24)
	2009	272 (80)	377 (132)	0	63 (30)
Viable seeds per ha ($x10^4$)	2007	24.74 (5.79)	8.77 (2.38)	0.05 (0.02)	0.23 (0.07)
	2008	44.53 (6.90)	39.17 (10.03)	0.07 (0.05)	0.17 (0.08)
	2009	20.21 (5.93)	12.71 (4.45)	0	0.20 (0.09)

Table C: Summary of results from the quasi-binomial generalised linear model of the proportion of viable black spruce seed. Bolded model terms indicate the response variable for each model. The intercept represents expected proportion of viable seed in forest stands and 2007. The model included forest zone and year as predictor variables. Bolded t-values indicate that a significant difference ($\alpha \leq 0.05$) was detected in the model.

Model term	Estimate	Standard error	t-value
Intercept	-1.05614	0.41766	**-2.529**
open forest	-0.38475	0.63837	-0.603
transitional forest	0.68267	0.51763	1.319
treed tundra	-0.08636	0.80183	-0.108
2008	-0.35565	0.46018	-0.773
2009	-1.88555	0.52519	**-3.590**
open forest*2008	-2.25988	0.88613	**-2.550**
transitional forest*2008	-0.30922	0.59709	-0.518
treed tundra*2008	-2.15924	1.02879	**-2.099**
open forest*2009	-16.73447	1731.19502	-0.010
transitional forest*2009	0.10711	0.65125	0.164
treed tundra*2009	0.20084	1.03725	0.194

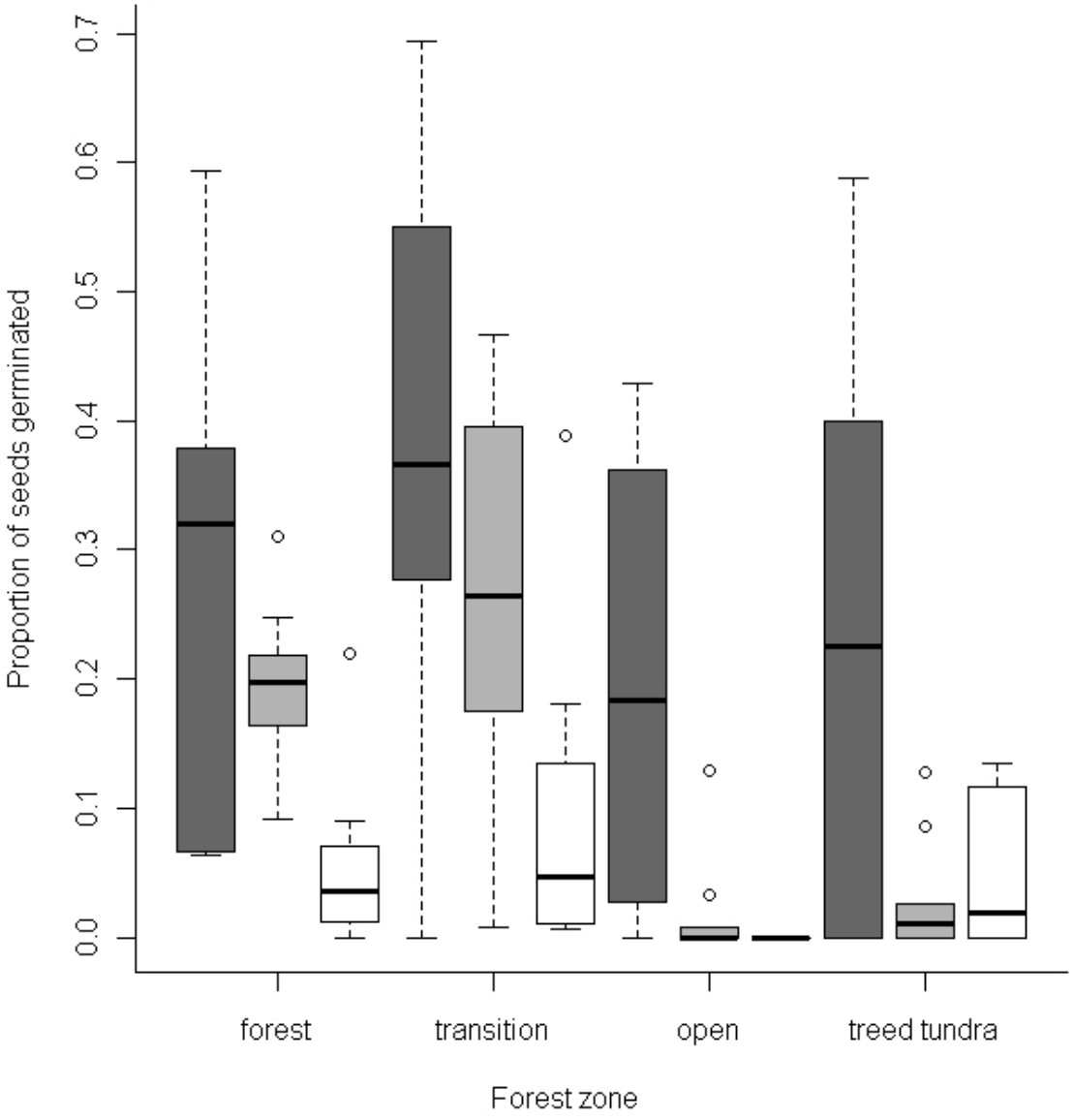

Figure 2-3: Proportion of seeds germinated in 2007, 2008, and 2009 (dark grey, light grey, and white boxes, respectively) in forest, transitional forest (transition), open forest (open), and treed tundra sites across the treeline ecotone in northern Yukon (n=3 sites/zone).

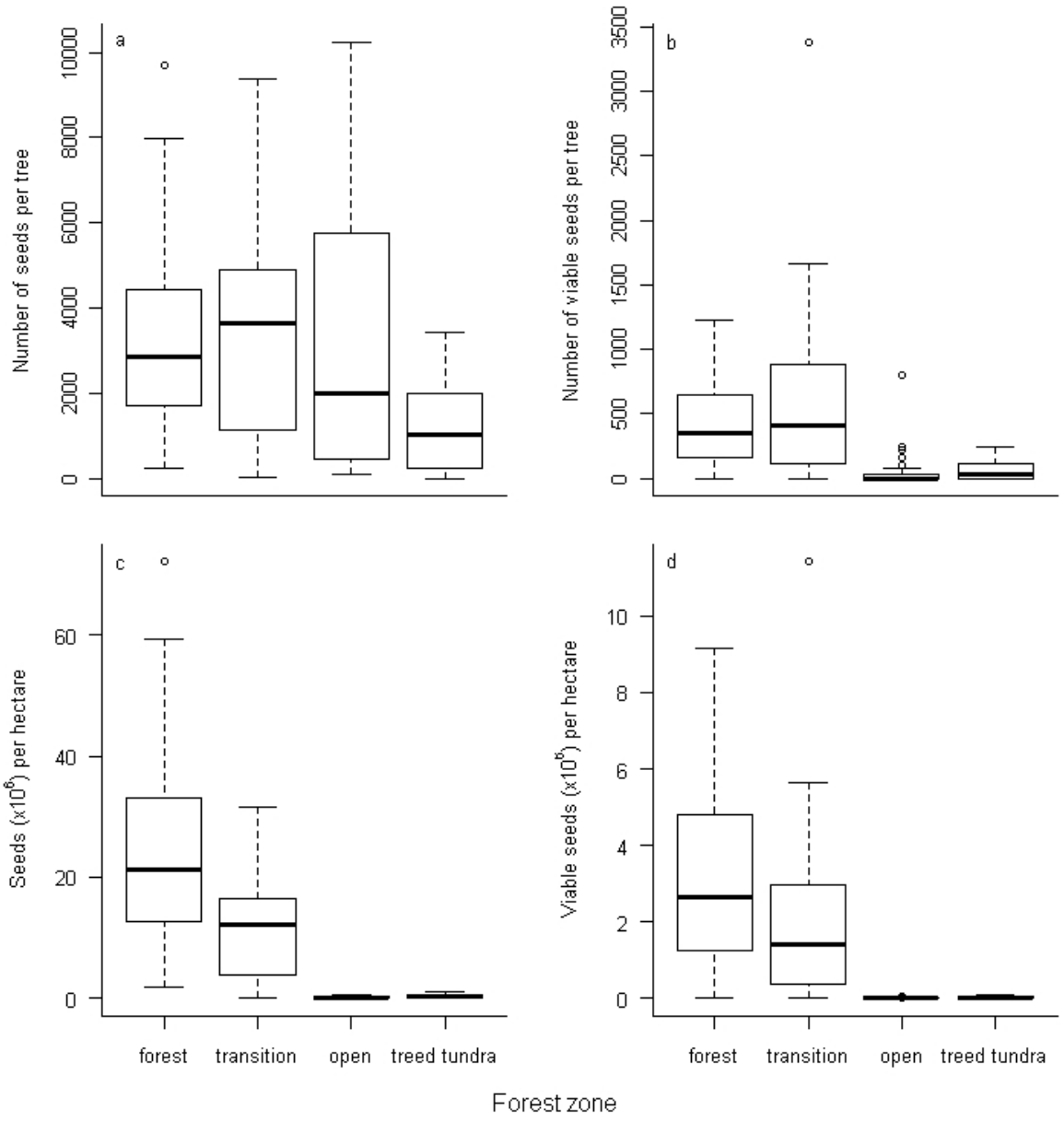

Figure 2-4: Number of seeds per tree (a), number of viable seeds per tree (b), number of seeds per hectare (c), and number of viable seeds per hectare (d) in forest, transitional forest (transition), open forest (open), and treed tundra sites across the treeline ecotone in northern Yukon (n=3 sites/zone).

(mean=20 ± 1 seeds/cone). There was no detectable difference in seed production per cone between individual trees sampled in forested sites ($F=1.55$, $df=9$, $p=0.14$). However, there was a significant difference in transitional forest ($F=2.48$, $df=9$, $p=0.01$), open forest ($F=2.71$, $df=9$, $p=0.008$), and treed tundra sites ($F=2.06$, $df=9$, $p=0.04$).

In addition to significant differences in reproductive potential across forest zones, analysis of tree-level data also indicated substantial tree-to-tree variability in cone and seed production. The proportion of seeds that germinated also varied between individual cones sampled in 2008, ranging from 0-1 in forest and transitional forest (means of 0.17±0.02 and 0.24±0.02, respectively), 0-0.2 in open forest (mean of 0.01±0.004), and 0-0.5 in treed tundra stands (mean of 0.03±0.01). The proportion of seeds that germinated differed significantly between individual trees in all four forest zones (forest: $F=2.17$, $df=9$, $p=0.03$; transitional forest: $F=4.67$, $df=9$, $p<0.0001$; open forest: $F=4.80$, $df=9$, $p<0.0001$; treed tundra: $F=2.30$, $df=9$, $p=0.02$).

As expected, there was some variation in the total number of cones produced per tree in 2008 (forest: 158±18; transitional forest: 95±21; open forest: 200 [only one individual sampled for cones]; treed tundra: 106±37) and 2009 (forest: 81±25; transitional forest: 112±28; open forest: 38±7; treed tundra: 158±33). The quasi-Poisson GLM indicated a significant interaction between forest zone and year, where individuals from treed tundra stands produced more cones than expected in 2009 ($t=2.33$, $df=1$, $p=0.02$). The model detected no statistical difference in the number of cones per tree between forest zones. Overall, there were significantly fewer cones produced in 2009 than 2008 ($t=-2.08$, $df=1$, $p=0.04$). .

2.3.2 Environmental characteristics

Analyses of environmental variables showed changes in environmental characteristics across the treeline ecotone. MANOVA indicated the multivariate response of depth of thaw and SOH thickness was significantly affected by forest zone (Pillai=0.82, approx. F=3.68, df=3, p=0.007) and microtopography (Pillai=0.85, approx. F=41.51, df=1, p<0.0001). Two-way ANOVA indicated that SOH thickness decreased from forest to treed tundra (F=4.85, df=3, p=0.01) and earth hummocks had thinner soil organic horizons than hollows (F=14.09, df=1, p=0.002; Figure 2-5a). Two-way ANOVA indicated that depth of thaw differed significantly between forest zones (F=8.51, df=3, p=0.001), where thaw was deepest in treed tundra sites (t=2.49, df=3, p=0.02; Figure 2-5b). Earth hummocks had deeper thaw than hollows (F=88.42, df=1, p<0.0001). Depth of thaw was negatively correlated SOH thickness (t=-5.61, df=22, p<0.0001; Figure 2-6). In contrast, MRPP indicated that the multivariate response of depth of thaw and SOH thickness did not differ between forest zones (MRPP chance-corrected within-group agreement = 0.027, *t* = -0.4, and p=0.28), although MRPP did detect a difference between microtopography (MRPP chance-corrected within-group agreement = 0.347, *t* = -10.02, and p<0.0001). Between-plot variance was greater for hummocks (average distance = 13.57) than hollows (average distance = 9.01).

2.4 DISCUSSION

Responses demonstrate a reduction in reproductive potential across the treeline in northern black spruce stands. The factors driving the observed gradient in reproductive potential were primarily the change in forest density, and secondarily, variations in seed viability and productivity per tree. For these reasons, spatial gradients in stand density are likely to be a key factor determining seed availability beyond the forest limit. Stand infilling (i.e., increases in

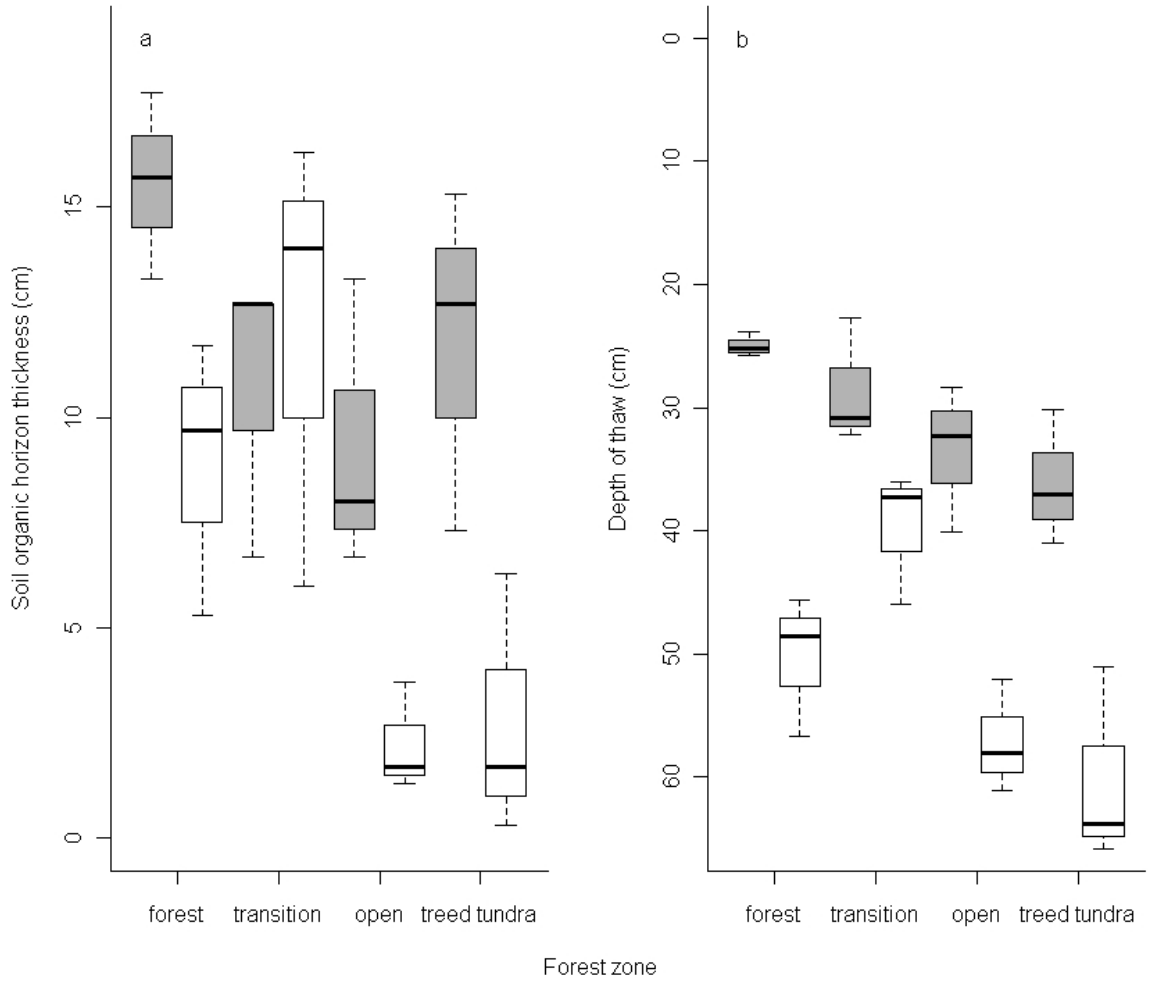

Figure 2-5: (a) Soil organic horizon thickness and (b) depth of thaw in forest, transitional forest (transition), open forest (open), and treed tundra sites across the treeline ecotone in northern Yukon (n=3 sites/zone). Sampling was stratified by hollow (grey) and hummock (white) microtopography. Depth of thaw is measured as depth below the ground surface, indicated by zero on the y-axis.

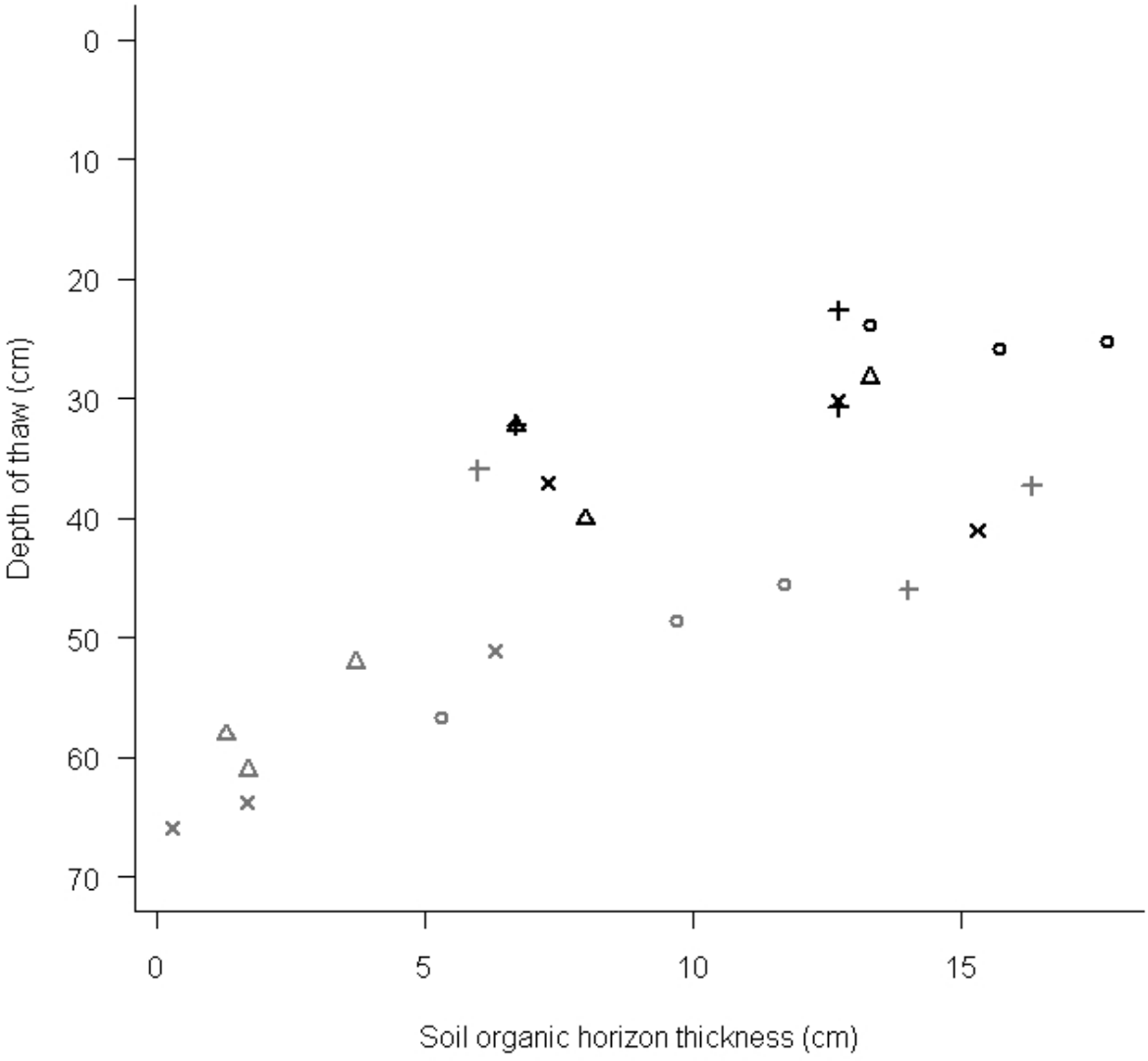

Figure 2-6: Bivariate relationship between soil organic horizon thickness and depth of thaw in forest (circles), transitional forest (+'s), open forest (triangles), and treed tundra (x's) sites across the treeline ecotone in northern Yukon. Sampling was stratified by hollow (black) and hummock (grey) microtopography. Each point represents the mean of six measurements per site, conducted in 2007. Depth of thaw is plotted as depth below the ground surface, indicated by zero on the y-axis.

density) near the treeline may thus be an important precursor to the development of sufficient seed inputs to allow subsequent treeline movement in response to climate. There have been widespread observations of stand infilling at treelines experiencing warming (e.g., see Danby & Hik, 2007; Harsch *et al.*, 2009; Harper *et al.*, 2011). Before landscape-scale expansion into tundra regions occurs, treeline stands may first undergo stand infilling, using forested stands as a major seed source. Following this infilling, sufficient seed would be present near tundra habitats for range expansion.

Even if seed production were equivalent for individuals across the treeline ecotone, the decrease in forest density would mean fewer seeds per hectare with an increase in latitude. Seed production was not equivalent between forested sites and transitional zones, further lessening the availability of viable seed at the northern margin of tree occurrence. The low reproductive potential of black spruce on the treed tundra suggests that forest stands are likely to act as the primary seed source for range expansion in treeline regions. This source-sink dynamic has also been observed in northern regions of the eastern boreal forest, where sparse viable seed at the northern most extent of tree occurrence means that forested stands are necessary for recruitment in treeline regions (Payette *et al.*, 1989; Sirois & Payette, 1989; Payette *et al.*, 2001).

Cone production in the study area was within the range observed in black spruce stands of northern Québec (range 0-2273, median 50 cones per tree; Sirois, 2000); however, the number of seeds per cone was greater than sites with similar forest density in the northern Québec. Forest and transitional forest stands had seed production of the same magnitude reported in Inuvik, Northwest Territories (6.03-13.2 x 10^5 seeds per ha; Black & Bliss, 1980), Minnesota (5.12-21.90 x 10^5 seeds per ha; LeBarron, 1948), and central Alaska and Yukon (5.97 x 10^5 seeds per ha in stands of similar age; Viglas, 2011). Seed production in treed tundra stands was one to two

orders of magnitude less than these reported values. This pattern has been observed in many northern woody species, including other stands of black spruce, white spruce, green alder (*Alnus viridis* subsp. *fruticosa* (Ruprecht) Nyman), and larch (*Larix laricina* (Du Roi); Elliott, 1979; Black & Bliss, 1980; Sirois, 2000; Lantz *et al.*, 2010). The observed reduction of seed production with increasing latitude further supports the hypothesis that environmental conditions, such as low air temperature, limit reproduction at treeline. Observational evidence in the study area suggests that survival of individuals in treed tundra sites is primarily due to clonal regeneration. No seedlings resulting from sexual reproduction were detected during the three-year field survey (Brown and Johnstone, unpublished data).

In contrast to cone production, we have presented empirical evidence of annual variation in seed viability in these northern black spruce stands. We cannot rule out that this variability was due to differences in individuals, as seed viability was not measured on the same black spruce trees annually. However, cone and seed production are influenced by many factors, including microsite conditions, local climate, genetic and ecological factors, and stand attributes (Owens & Blake, 1985; Zasada *et al.*, 1992; Sirois, 2000). Factors that influence the production of cones may not be the same as those that influence seed production or viability. Cone production is greatly influenced by conditions occurring in the year of bud initiation (Kramer, 1960). Seed viability is, in part, affected by the production of male cones and release of pollen. Pollen cone production is related to the previous year's conditions, but pollen release and dispersal is affected by local climatic conditions at the time of staminate-cone dehiscence. Warm and dry conditions may increase pollen dispersal, whereas wet conditions could potentially reduce dispersal distance.

It is important to consider genetic differentiation between populations when discussing the potential for the expansion of a population's range (Linhart & Grant, 1996), particularly when individuals occur along a gradient. Populations at the edge of a species' distribution, where there are fewer individuals and inbreeding can be more common, can have lower genetic diversity than populations at the centre of the distribution (Gapare & Aitken, 2005). Black spruce exhibit a large amount of adaptive variation between populations, which correlates with geographic and climatic factors (Khalil, 1984; Park & Fowler, 1988; Morgenstern & Mullen, 1990; Parker *et al.*, 1996). Even within what would appear to be the same population, groups of black spruce in contrasting habitats can have different genetic structure (Boyle *et al.*, 1990). Black spruce populations from across the species' range show differences in, for e.g., the degree of cone serotiny, the age of first cone and seed production, and phenology (Morgenstern 1978; Zasada *et al*., 1992; Parker *et al*., 1994; Beaulieu *et al*., 2004; Viglas, 2011). Black spruce seed viability decreases as the cone ages (Zasada *et al.*, 1992; Viglas, 2011). In the absence of fire, the cones open with age (Zasada *et al.*, 1992), meaning that seed dispersing from unburned northern forests into treeline sites may have relatively low viability, depending on the degree of cone serotiny. Cones with resin that is slow to degrade may have less viable seed to disperse than younger cones, reducing the number of seeds that may establish. Seed production and seedling establishment beyond the northern edge of black spruce's range could also be hindered if the phenologies of reproductive processes in individuals from northern and marginal stands are misaligned.

As I have described, northern treelines are ecotones created by environmental conditions that are adverse for tree survival, growth, and/or reproduction (Holtmeier & Broll, 2005). In the northern black spruce treeline studied here, I have identified environmental variables that change

across the treeline gradient, which may be linked to successful tree establishment and growth. Within a forest zone, depth of thaw was greater on earth hummocks than hollows, a trend previously observed in black spruce stands in Northwest Territories (Black & Bliss, 1980) and that is likely a function of SOH thickness. SOH thickness also likely contributed to deeper summer thaw in treed tundra than transitional forest stands, a pattern that was more obvious on earth hummocks than hollows. Although treed tundra had deeper summer thaw than transitional forest stands, it is the combination of interacting environmental factors that deteriorate conditions for tree establishment, growth, and reproduction from forest to treed tundra, i.e., exposure to harsh winds and low snow cover in tundra sites.

Seed availability is not the only requirement for range expansion; there must also be a suitable seedbed for recruitment. In the study area, the reproductively mature black spruce stands are dominated by a moss and lichen understory across the treeline ecotone (Brown and Johnstone, unpublished data). Numerous studies have demonstrated that mosses and lichens are a poor seedbed for black spruce recruitment, predominately because of their porous nature and unstable moisture conditions (e.g., Charron & Greene, 2002; Jayen *et al.*, 2006). These poor seedbeds may mean that large amounts of seed would be required to expand the range limits of the black spruce stands studied here. Treeline expansion may then occur via large increases in seed production or changes in the recruitment success of those seeds due to increases in seedbed quality or favourable climate for survival.

2.4.1 Conclusions

I have identified a reduction in the reproductive potential of black spruce across the treeline ecotone in northern Yukon. Further research is needed to link annual variability in seed production and viability to local climatic and environmental conditions. This research indicates

that northern forest stands may act as a seed source for treeline stands, thus the dynamics of northern forest stands will play a key role in future treeline change in this region of the sub-arctic.

3.0 REPEAT FIRES REDUCE SEED AVAILABILITY AND ALTER SUBSTRATE CONSTRAINTS ON BLACK SPRUCE REGENERATION

FOREWORD

Whereas Chapter 2 summarized the structure and reproductive potential of treeline forests that have undergone the historic fire regime in the study area, in this chapter I document the impact of an altered disturbance regime on black spruce forest regeneration. Field experimentation using seeding trials is combined with monitoring of seed rain to identify the ecological mechanisms that drive patterns of forest recruitment in response to fire disturbance in northern black spruce forests. This chapter is modified from:

Brown, C.D. and Johnstone, J.F. Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on black spruce regeneration. *In preparation*. Forest Ecology and Management.

3.1 INTRODUCTION

The Earth has entered a period of rapid climate change that will have broad impacts on the structure and function of ecological systems (Millennium Ecosystem Assessment, 2005). Climate change will impact ecosystems through direct temperature effects and indirect effects caused by changes to disturbance regimes, such as increased fire frequency. Disturbance characteristics exert a strong control over ecosystem structure and function, and the consequences of changing disturbance regimes for ecosystems and communities are a priority for global change research (Turner, 2010). Species that have adapted to regenerate with a specific disturbance regime frequency are particularly sensitive to disruptions to that regime (Lamont *et al.*, 1991). Serotinous species have adapted regeneration strategies that allow for pulses of regeneration following fire within the fire regime they have historically experienced (Lamont *et al.*, 1991; Lamont & Enright, 2000). A disruption of that regime reduces the advantage of a serotinous regeneration strategy, particularly if a fire occurs before the species has reached reproductive maturity. Consequently, changes in the frequency of disturbance can disrupt dominance hierarchies even in the absence of additional environmental change (Paine *et al.*, 1998; Bond *et al.*, 2005).

Constraints on succession caused by a disruption to the fire regime have been detected in serotinous systems globally (e.g., Keeley *et al.*, 1999; Johnstone & Chapin, 2006b). In the boreal forest, many tree species exhibit serotinous regeneration strategies, since fire is the dominant initiator of secondary succession in the boreal forest (Payette, 1992). Air temperatures are increasing in northern boreal regions (Chapin *et al.*, 2005) and, although climate-fire interactions are complex, models consistently predict that fire activity will increase in the boreal forest due to

climate change (Balshi *et al.*, 2009; Flannigan *et al.*, 2009). Such changes to the fire regime have already been observed in many areas of the circumboreal forest (Flannigan *et al.*, 2009).

Black spruce (*Picea mariana* [Mill.] B.S.P.), like many boreal conifers, maintain seeds in an aerial seed bank of semi-serotinous cones for dispersal after fire (Lamont *et al.*, 1991). The individuals that establish during the first five to ten years following fire, when seed viability and nutrients are at their highest, make up the majority of the stand that burns during the next fire (Johnson & Fryer, 1989). It can take two to three decades for black spruce to reach reproductive maturity and have viable seed available for post-fire self replacement (Burns & Honkala, 1990). In the western boreal forest, the interval between fires has historically been 80 to 150 years (Viereck, 1983; Larsen, 1997), by which time black spruce have reached reproductive maturity and produced enough seed to self replace after fire. Post-fire regeneration depends on seed availability and seed bed quality. Soil temperature and moisture, soil organic horizon thickness, and understory competition are all affected by fire history (Kasischke & Johnstone, 2005), and contribute to the ability of a seed to germinate and survive in a given location (Eriksson & Ehrlen, 1992; Greene *et al.*, 1999). Changes in disturbance that affect seed availability or seed bed quality have the potential to alter patterns of post-fire recruitment and succession (Lloret *et al.*, 2003; Johnstone & Chapin, 2006b; Caplat & Anand, 2009).

My objective was to quantify the impacts of different fire return intervals on processes that may constrain black spruce replacement after fire. I hypothesized that black spruce recovery in stands experiencing a short fire return interval (14-15 years) would be reduced due to the lack of an aerial seed bank produced by the local, immature trees. I anticipated that these effects on seed availability would be more important than substrate quality in limiting recruitment after a short-interval fire. In contrast, I hypothesized that poor conditions for seed germination and

survival would limit seedling recruitment in unburned stands. I tested these hypotheses by documenting patterns of seed availability and seedling recruitment in stands of varying fire history. This study addresses an important gap in our understanding of the consequences of changes in fire regime to successional dynamics in fire-prone forests. This research provides strong empirical evidence of ecological mechanisms that may drive rapid changes in forest composition in a region currently experiencing climatic warming (Chapin *et al.*, 2005) and associated increases in fire activity (Kasischke & Turetsky, 2006).

3.2 METHODS

3.2.1 Study area

I established a field experiment in a natural mosaic of stands differing in recent fire history. Study sites were located in sub-arctic forests dominated by black spruce near Eagle Plains in northern Yukon Territory, Canada (66°06'56"N, 137°16'11"W). The region is characterized by rolling hills with fine grained loess soils over weathered bedrock (Smith *et al.*, 2004). The surface microtopography is dominated by small-scale earth hummocks formed by differential freezing and thawing of soil (Kokelj *et al.*, 2007). Soils are underlain with continuous permafrost with a seasonal thaw depth of less than 1 m (Tarnocai *et al.*, 1993). Eagle Plains has a continental climate. The nearest weather stations, in Dawson City (~290 km SW; 64^{o}02'35"N, 139^{o}07'40"W) and Old Crow (~190 km NW; 67^{o}34'14"N, 139^{o}50'21"W) YT, have mean annual air temperatures of -4.4°C and -9°C (Environment Canada, 2011). The mean annual precipitation is 324 mm in Dawson City and 266 in Old Crow, about half of which falls as rain in the summer in both locations (Environment Canada, 2011). Vegetation in the region is dominated by black spruce in the forest canopy with an understory of evergreen shrubs, willows (*Salix* spp.), and *Sphagnum* and feather mosses (e.g., *Hylocomium* spp.; Russell *et al.*, 1992).

The fire history mosaic at Eagle Plains allowed for the sampling of mature unburned forests and forests that burned after long or short fire-free intervals, all within close proximity to one another (Figure 3-1). In 1990 and 1991, two adjacent regions of Eagle Plains were burned during lightning-ignited fires (1990: 33,500 ha and 1991: 4,800 ha). A third fire burned the area in 2005 (69,000 ha), partially overlapping both the 1990 and 1991 burns. Fire Weather Index and Fire Behaviour Prediction values (Wagner, 1987; Lee, 1995) calculated for the study area for a two week period surrounding the date of ignition of each fire suggested that the 2005 fire burned in more volatile conditions than the 1990 and 1991 fires (R. Carr and P. Englefield, unpublished data; see Chapter 5 for additional information). The period of the 2005 fire had several individual days of higher Fire Weather Index values than the 1990 and 1991 fire periods, which is reflected in the sizes of each fire. Index values were calculated by the Canadian Forest Service, Northern Forest Centre, using weather data and the Spatial Fire Management System, an extension of ArcView (Esri, Redlands, California, U.S.A.). Since the study region is remote, these values were calculated using weather stations in Dawson City and Old Crow, Yukon, and Fort McPherson, Northwest Territories. Thus, there is an amount of uncertainty associated with the index values. Despite the difference in estimated conditions during the time of ignition, all three fires were of low-moderate severity in long-interval burned stands, as indicated by the presence of fine branches on fire-killed trees. Sites in three stages of post-fire forest recovery were selected for study: 1) mature, unburned forest representing a long fire-free interval (previous fire ~77 years ago; MF), 2) early successional stands following a long-interval burn (fire in 2005 following ~94 years fire-free; LI), and 3) early successional stands following a short-interval burn (fire in both 1990/91 and 2005; SI).

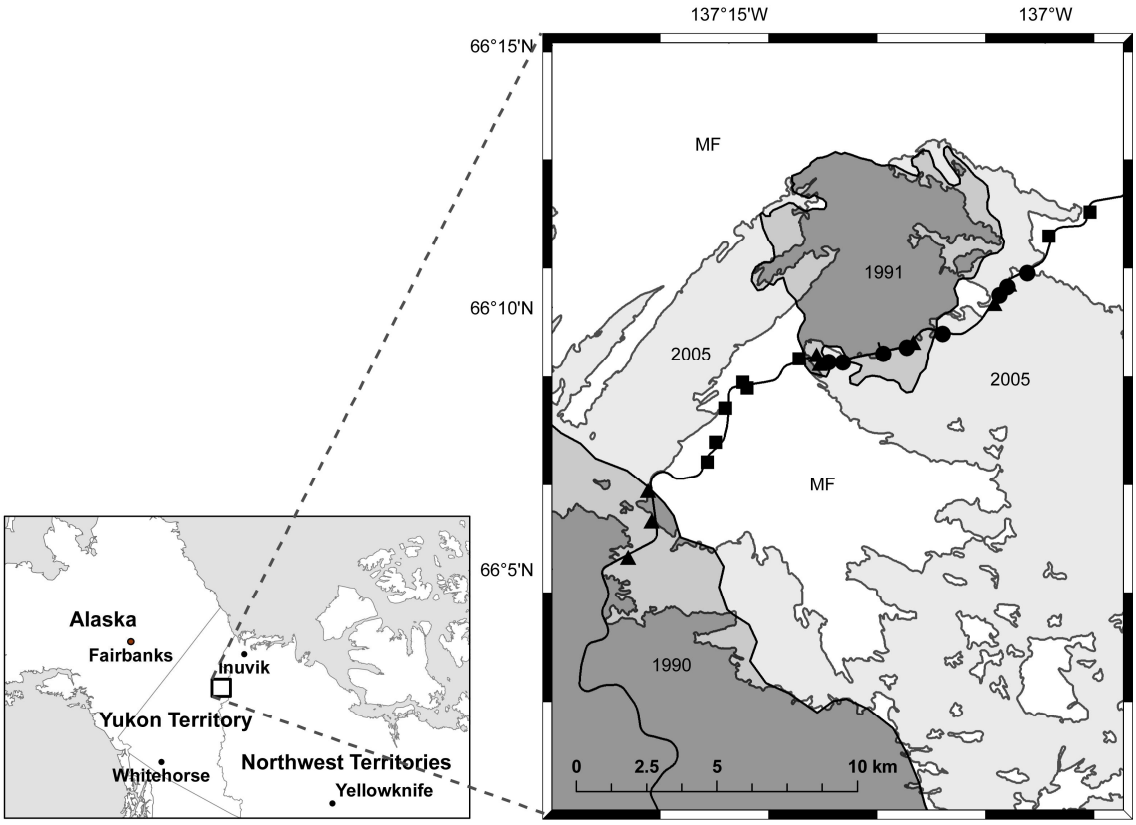

Figure 3-1: Study area in northern Yukon, Canada, with areas burned in 1990/1991 (dark grey), 2005 (light grey), and the 1990s and 2005 fire overlap (medium grey) indicated. Mature forest (MF) is indicated in white. Study sites (n=8 per fire history) were established in mature, unburned forest (squares), early successional long-interval burns (circles), and early successional short-interval burns (triangles).

3.2.2 Field measurements

I overlaid an experimental manipulation on the natural treatment contrasts created by the fire history mosaic of the study area, incorporating seed traps and seeded plots in a two-factor design. Eight 30 m x 30 m sites were selectively placed within each fire history class (MF, LI, and SI). Each site contained three east-west transects composed of seed traps and seeded plots.

Six seed traps were positioned randomly along one 30 m east-west transect in each site. Seed traps consisted of a 50 cm x 25 cm x 5.7 cm deep plastic greenhouse tray with a piece of plastic artificial grass fastened to the bottom, to reduce wind scouring of trap contents (Johnstone *et al.*, 2009). Each seed trap covered 0.125 m^2 of ground, thus the six traps sampled a 0.75 m^2 area in each experimental site. Seed traps were emptied as early as possible in June after snowmelt in 2008 and 2009 to prevent the seeds from germinating in the traps. A second annual collection of seeds was made at the end of each summer, in August 2008 and 2009. The final seed trap collection occurred in mid-July 2010.

I measured viability of black spruce seed collected in the seed traps using laboratory germination trials (Leadem *et al.*, 1997). Contents from the six traps per site were pooled into a single sample and hand sorted to separate black spruce seed from other debris. The sorted samples were placed on moist filter paper in a Petri dish (9 cm diameter) at the beginning of the germination trial and were watered once per day with deionised water. Each site was tested in a separate dish, except where samples had more than 100 seeds and were divided into multiple dishes. Seeds were allowed to germinate for 28 days at 18 hours of light per day at room temperature (~20°C). Seeds were considered germinated when their hypocotyl grew to twice the length of the seed coat (Leadem *et al.*, 1997).

Site differences in potential seedling recruitment were assessed with experimental applications of black spruce seed. In each site, 10-0.5 m x 0.5 m sub-plots were seeded with 0.3

g (~250 seeds) of viable black spruce per sub-plot. Seeded plots were positioned at even intervals along two 30 m transects and were stratified by microtopography, with five plots located on earth hummocks and five positioned in hollows. Each seeded plot was paired with an adjacent control plot to which no seeds were added. Seeds were evenly spread by hand across the surface of the forest floor in late summer (16-17 August 2007 and 6-7 August 2008) to allow for winter stratification of the seed prior to germination the following spring. Separate sub-plots were seeded in 2007 and 2008 to distinguish annual effects on potential emergence. The seed used in the trial was collected from sub-arctic black spruce forests in Tok, Alaska (~63°19'N, ~142°58'W). Emergent seedlings in seeded and control plots were counted in June, July, and August in 2008 and 2009, and in July 2010. Because seedlings were monitored regularly, I was able to detect new seedlings as they emerged and distinguish between recent seedlings and older recruits.

Basal area and density of black spruce stems were measured at each experimental site to characterize stand structure and seed source strength (Greene & Johnson, 1999). Pre-fire stems were measured in burned sites whereas living stems were measured in mature stands. As nearly no wood biomass remained in the short-interval stands, and thus no seed source, I measured the distance from the edge of each short-interval stand to the nearest black spruce seed source. Seed source was defined as a stand of >20 living or recently burned (in the 2005 fire) mature black spruce. Distances were measured rounded to the nearest metre using a hand-held GPS (error ± 6 m).

3.2.3 Statistical analyses

Results from the seed trap collections and germination trials were summarized as total and viable annual seed rain per site. All individual seedlings that emerged within a plot during

the study period were summed to calculate the total number of seedlings regardless of whether they survived past emergence. Individuals that survived at least two years were counted as two-year recruits. I analysed data on total seedlings and two-year recruits separately. Only total seedlings are presented for plots seeded in 2008, since two years had not passed between initial emergence after seeding and the last measurements. For all seeded plots, counts of total seedlings and two-year recruits were corrected by subtracting the counts from control plots within the same site. Correcting the seeded counts did not change the qualitative impacts of fire history and allowed me to examine the seeding effect alone, without contributions from background natural recruitment.

Analyses of the seed trap data were conducted with generalised linear models (GLMs) using raw count data. Because of the structure of count data, I first constructed a model for each response variable from the seed trap data (total seed and viable seed) using GLMs with Poisson distributions, incorporating the natural logarithm as the link function (Zuur *et al.*, 2009). I then ran the two models using GLMs with negative binomial error distributions. In both cases, a likelihood ratios test led me to select negative binomial models over Poisson distributions to account for over dispersion due to extra variation in the count data (Zuur *et al.*, 2009). Seed rain models included fire history class as the predictor variable.

Seedling emergence data were also analysed with GLMs using raw count data. The two, individually modelled response variables (total seedlings and two-year recruits) each had a large number of zeros observed, which is common in ecological data. I used zero-altered or hurdle models to deal with the excess number of zeros (Zuur *et al.*, 2009). Zero-altered models consist of two parts. The data are first modelled as presence/absence of black spruce in a binomial model. Non-zero observations are then modelled with a truncated Poisson model (Zuur *et al.*,

2009). As with the seed trap data, I first constructed a model for each response variable from the seeded plots (total seedlings and two-year recruits) using zero-altered models with Poisson distributions (ZAPs), incorporating the natural logarithm as the link function (Zuur *et al.*, 2009). I then ran the two models using zero-altered models with negative binomial error distributions (ZANBs). In both cases, a likelihood ratios test led me to select ZANBs over ZAPs to account for over dispersion due to extra variation in the count data (Zuur *et al.*, 2009).

Both ZANB models (total seedlings and two-year recruits) had different predictor variables for the binomial model and count models, which I selected using standard model selection methods (Zuur et al., 2009). When modelling total seedlings, I included fire history, microtopography, seeding treatment, and an interaction term for fire history and seeding treatment as predictor variables. The count model of total seedlings included the same predictor variables, with the addition of an interaction term for fire history and microtopography. The binomial model of two-year recruits included fire history and microtopography as predictor variables. The count model of two-year recruits included the same predictor variables, with the addition of microtopography and an interaction term for fire history and microtopography. In each model, the intercept represented expected seedling counts in LI stands, hollows, and unseeded control plots.

I assessed model fit using residual diagnostics (Zuur *et al.*, 2009). All statistical analyses were conducted with R (R Development Core Team, 2009) using the "MASS" package for negative binomial GLMs (Venables & Ripley, 2002), the "pscl" package for zero-altered models (Zeileis *et al.*, 2008; Jackman, 2010), and the "lmtest" package for likelihood ratios tests (Zeileis & Hothorn, 2002).

3.3 RESULTS

3.3.1 Seed rain

Total (X^2=87.00, df=2, p<0.001) and viable (X^2=13.35, df=2, p=0.001) black spruce seed rain counts differed significantly among fire history classes (Table 3-1). This difference was due to SI stands, which had lower counts of total (z=-8.83, p<0.001) and viable (z=-4.73, p<0.001) black spruce seed than MF and LI stands. These differences were apparent for seeds collected in all years (2008-2010). Total and viable black spruce seed rain did not differ between MF and LI stands in any year (p>0.05; Table 3-1). The mean percent viability did not differ in MF, LI, and SI stands (8.0 ± 1.5%, 6.5 ± 0.9%, and 7.2 ± 4.8%, respectively; F=0.066, df=2, p=0.93).

3.3.2 Total emergence

Fire history, microtopography, and seeding treatment had significant effects on patterns of seedling emergence (Tables 3-2 and 3-3). The total number of seedlings was consistently lowest in MF stands and in control plots. Total seedlings in control plots, representing emergence from natural seed sources, was greatest in LI stands (Figure 3-2a, Table 3-2). MF and SI stands had relatively little natural emergence over the three years of measurements. The binomial model, which was built upon presence/absence data, indicated that LI stands had significantly more plots with black spruce seedlings present than SI or MF stands, and hollows had significantly more plots with black spruce than earth hummocks. There was a significant interaction between fire history and seeding treatment. Adding seed to SI and MF stands changed the sign of the model estimate from negative to positive, meaning that seeded SI and MF stands tended to have black spruce seedlings present while control plots in those stands did not. This applied to SI stands seeded in 2007 and SI and MF stands seeded in 2008.

The count model indicated that in sites where black spruce seedlings grew, LI stands had significantly more seedlings than SI or MF stands, and hollows had significantly more

Table D: Summary of total and viable seed rain across fire history classes (MF=mature forest, LI=long-interval burned, and SI=short-interval burned; n=8 sites per fire history class with 0.75 m^2 sampled in each site). Data are means with standard error shown in parentheses. Bolded values indicate that the category differed significantly ($\alpha \leq 0.05$) from all others in the negative binomial count model.

	Total[1] seed rain per m^2			Viable[2] seed rain per m^2		
Year collected	MF	LI	SI	MF	LI	SI
2008	64.5 (19.1)	99.3 (15.4)	**10.2 (3.7)**	2.3 (0.6)	4.3 (1.1)	**0.3 (0.2)**
2009	49.7 (7.7)	52.7 (8.2)	**6.9 (1.9)**	5.4 (1.5)	5.3 (1.3)	**0.9 (0.9)**
2010	68.8 (15.9)	72.0 (12.6)	**9.0 (2.4)**	1.4 (0.4)	2.0 (0.6)	**0.1 (0.1)**
Average	61.0 (11.5)	74.7 (7.3)	**8.7 (1.2)**	5.3 (0.7)	6.4 (1.0)	**1.9 (0.4)**

[1] total number black spruce collected during each sample period

[2] number of black spruce seed that germinated during each sample period

Table E: Summary of total seedlings and two-year recruits counted in experimentally seeded plots in the three fire history classes (MF=mature forest, LI=long-interval burned, and SI=short-interval burned; n=8 sites per fire history class with 1.25 m^2 sampled for each seed treatment-microtopography combination in each site). Data are also summarized by microtopography within each fire history class, with sites located either on earth hummocks or in hollows in hummocky terrain. Counts in seeded plots were corrected by subtracting the counts from control plots within the same site. Mean data are presented with standard error shown in parentheses.

	MF			LI			SI		
	overall	hollow	hummock	overall	hollow	hummock	overall	hollow	hummock
total seedlings									
control	0.7 (0.3)	1.3 (0.4)	0.1 (0.1)	10.3 (2.0)	14.0 (3.4)	6.6 (1.0)	0.7 (0.2)	0.8 (0.4)	0.6 (0.3)
2007 seeded	8.1 (3.3)	7.9 (3.8)	6.9 (5.3)	62.1 (9.3)	67.5 (14.4)	36.0 (8.2)	38.3 (14.9)	51.6 (27.9)	23.5 (10.7)
2008 seeded	3.7 (1.3)	2.8 (1.3)	3.9 (2.1)	33.3 (5.1)	32.5 (8.3)	14.5 (3.7)	15.1 (6.2)	20.6 (12.1)	8.1 (2.6)
two-year recruits									
control	0 (0)	0 (0)	0 (0)	5.3 (1.4)	7.4 (2.4)	3.1 (0.7)	0.1 (0.1)	0.3 (0.2)	0 (0)
2007 seeded	3.0 (1.7)	2.4 (1.1)	3.6 (3.3)	29.6 (4.8)	31.3 (7.8)	17.4 (4.2)	19.2 (9.5)	30.1 (18.3)	8.0 (3.9)

Table F: Summary of results from the zero-altered negative binomial model of total black spruce seedlings (d.f.=23). Both models included fire history class, microtopography, seeding treatment, and the interaction between fire history class and seeding treatment as predictor variables. The count model also included the interaction between fire history class and microtopography as a predictor variable. For seeded plots, the models were based on counts corrected by subtracting counts from control plots within the same site. The intercept represents expected seedling counts in LI stands, hollows, and unseeded control plots. Bolded values indicate that a significant difference ($\alpha \leq 0.05$) was detected in the model.

	Binomial model			Count model		
Model term	Estimate	Standard error	z-value	Estimate	Standard error	z-value
Intercept	1.2223	0.2660	**4.595**	0.6889	0.2218	**3.105**
SI	-3.0806	0.4503	**-6.842**	-1.7466	0.7527	**-2.321**
MF	-3.0806	0.4503	**-6.842**	-1.9607	0.7414	**-2.645**
hummock[1]	-0.8063	0.1781	**-4.528**	-0.5807	0.2080	**-2.792**
seeded 2007[2]	0.6158	0.3746	1.644	1.9412	0.2529	**7.674**
seeded 2008[3]	-0.2878	0.3400	-0.846	1.3600	0.2653	**5.126**
SI*hummock	-	-	-	0.1602	0.3676	0.436
MF*hummock	-	-	-	0.9723	0.4584	**2.121**
SI*seeded 2007	1.4892	0.5777	**2.578**	1.9083	0.7848	**2.432**
MF*seeded 2007	0.9445	0.5823	1.622	0.2272	0.8069	0.282
SI*seeded 2008	2.3928	0.5564	**4.300**	1.3465	0.7906	1.703
MF*seeded 2008	1.1926	0.5772	**2.066**	0.2774	0.8499	0.326

[1]Plots located on hummock microtopography

[2]Plots seeded with black spruce in August, 2007

[3] Plots seeded with black spruce in August, 2008

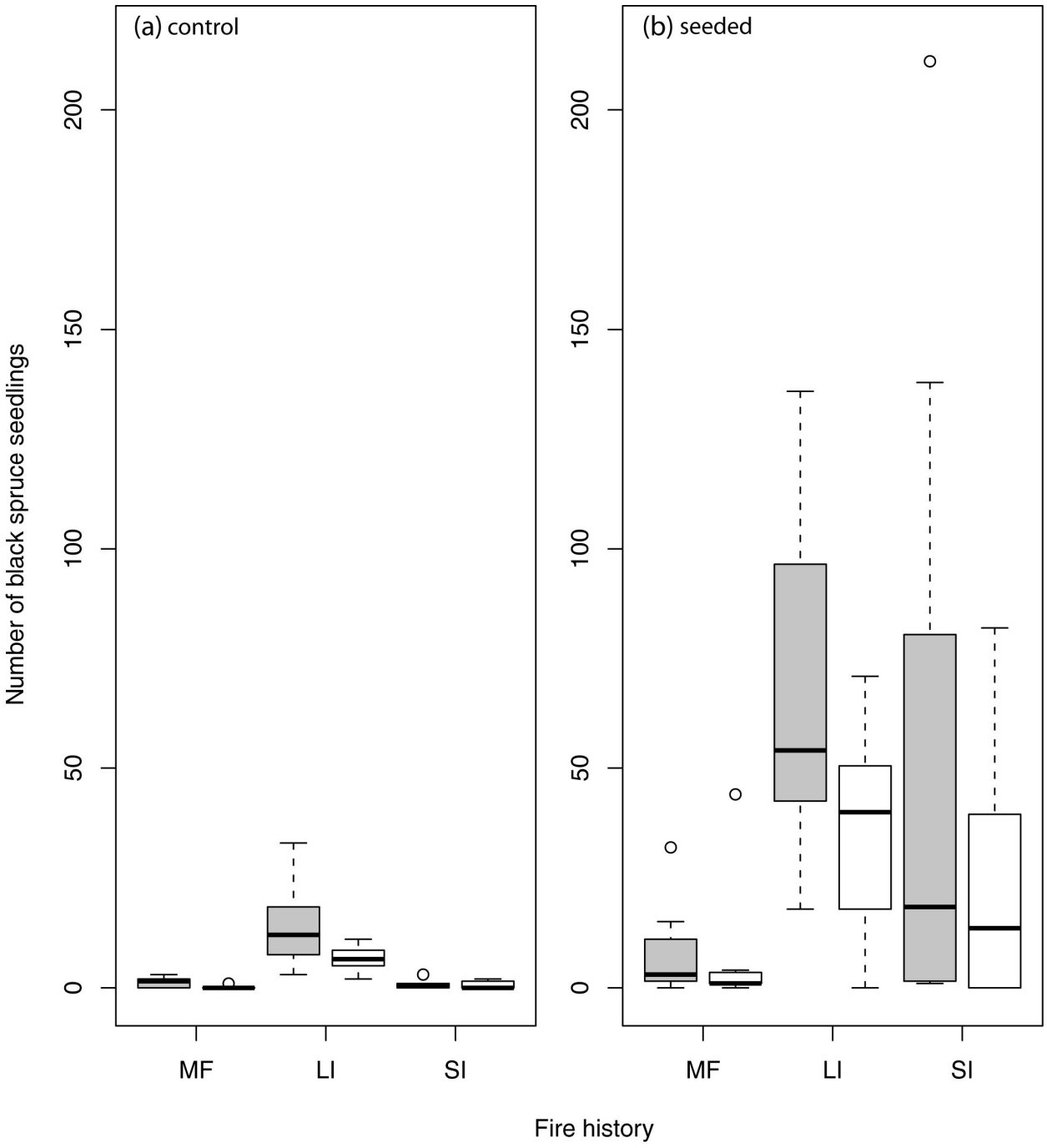

Figure 3-2: Total number of black spruce seedlings (a=control, b=seeded plots), grouped by fire history and microtopography. Fire history classes are: MF=mature forest, LI=long-interval burned, and SI=short-interval burned (n=8 sites per fire history class with 1.25 m^2 sampled for each seed treatment-microtopography combination in each site). Grey boxes indicate sites located in hollows within hummocky terrain and white boxes indicate sites located on earth hummocks. Data for seeded plots (b) have been corrected by subtracting the number of black spruce germinants in control plots in order to show the seeded effects.

seedlings than hummocks. Adding black spruce seed resulted in significantly more seedlings than occurred due to natural recruitment (Figure 3-2b). The effect of seeding on total seedlings was consistent for both 2007 and 2008 seeded plots (Tables 3-2 and 3-3). There was a significant interaction between fire history and microtopography. When black spruce seedlings were present in MF stands, more were found on earth hummocks than in hollows. There was also a significant interaction between fire history and seeding treatment, as was detected in the binomial model. In the count model, however, this interaction was only significant for SI stands seeded in 2007.

3.3.3 Two-year recruits

Fewer black spruce survived to two years than originally emerged in the plots (Table 3-2). However, as with total seedlings, fire history, microtopography, and seeding treatment had significant effects on patterns of two-year recruits (Tables 3-2 and 3-4). The binomial model and the count model both indicated that the number of two-year recruits was lowest in MF stands and in control plots. I consistently found more two-year recruits in LI stands than in MF or SI stands. No natural two-year recruits were detected in MF stands, and only two were found in SI stands. Both models showed that the presence of two-year recruits was significantly more likely in plots that had been seeded. The count model also indicated that two-year recruits were present significantly more in hollows than on earth hummocks, similar to the total germinants models. However, as seen in the count model for total germinants, there was a significant interaction between fire history and microtopography. When two-year recruits were present in MF stands, more grew on earth hummocks than in hollows.

Table G: Summary of results from the zero-altered negative binomial model of two-year old black spruce recruits (d.f.=12). Both models included fire history class and seeding treatment as predictor variables. The count model also included microtopography and the interaction between fire history class and microtopography as predictor variables. For seeded plots, the models were based on counts corrected by subtracting counts from control plots within the same site. The intercept represents expected seedling counts in LI stands, hollows, and unseeded control plots. Bolded values indicate that a significant difference ($\alpha \leq 0.05$) was detected in the model.

	Binomial model			Count model		
Model term	Estimate	Standard error	z-value	Estimate	Standard error	z-value
Intercept	-0.5902	0.2132	**-2.769**	0.2414	0.3482	0.693
SI	-2.2632	0.3031	**-7.467**	0.6346	0.4414	1.438
MF	-3.0168	0.3550	**-8.497**	-2.1785	0.5953	**-3.659**
hummock[1]	-	-	-	-0.7828	0.3201	**-2.445**
seeded[2]	1.8613	0.2793	**6.664**	1.6732	0.3371	**4.963**
SI*hummock	-	-	-	-0.4547	0.6451	-0.705
MF*hummock	-	-	-	2.3544	0.8934	**2.635**

[1]Plots located on hummock microtopography

[2]Plots seeded with black spruce in August, 2007

3.3.4 Site measurements

The pattern of basal area and distance to seed source in the study sites reflect the fire history of the study area (Figure 3-3). Due to the absence of woody biomass after two closely timed fires, SI stands had 0 m^2/ha of standing dead black spruce and a mean distance of 71 ± 16 m to the nearest seed source. MF and LI stands, which had living and dead standing black spruce, respectively, had 0 m distance to the nearest seed source and basal areas of 7.9 ± 1.1 and 13.0 ± 1.9 m^2/ha, respectively (Figure 3-3). Based on published equations relating stand basal area to seed production of black spruce (Greene & Johnson, 1999), these basal areas would be expected to represent an average of 184 and 296 seeds per m^2 in MF and LI stands, respectively.

3.4 DISCUSSION

Observed patterns of seed rain and seedling recruitment are consistent with the hypothesis that seed availability limits black spruce regeneration after two closely timed fires. Post-fire regeneration from natural seed was reduced in MF and SI stands compared to LI stands. Once seed was added, regeneration in SI stands was equivalent or superior to that in LI stands. MF stands had little recruitment, even when seed was experimentally added. The contrast between the responses to seeding in SI versus MF stands indicates that seedling regeneration in the different stand types is limited by different factors. These results indicate that recruitment in SI stands is limited by seed availability, while recruitment in unburned, MF stands is limited by seed bed quality.

These constraints on seedling recruitment are key ecological mechanisms driving fire and vegetation interactions in these forests. Firstly, constraints on seed germination in unburned stands means that cycles of seedling recruitment and stand renewal are primarily restricted to

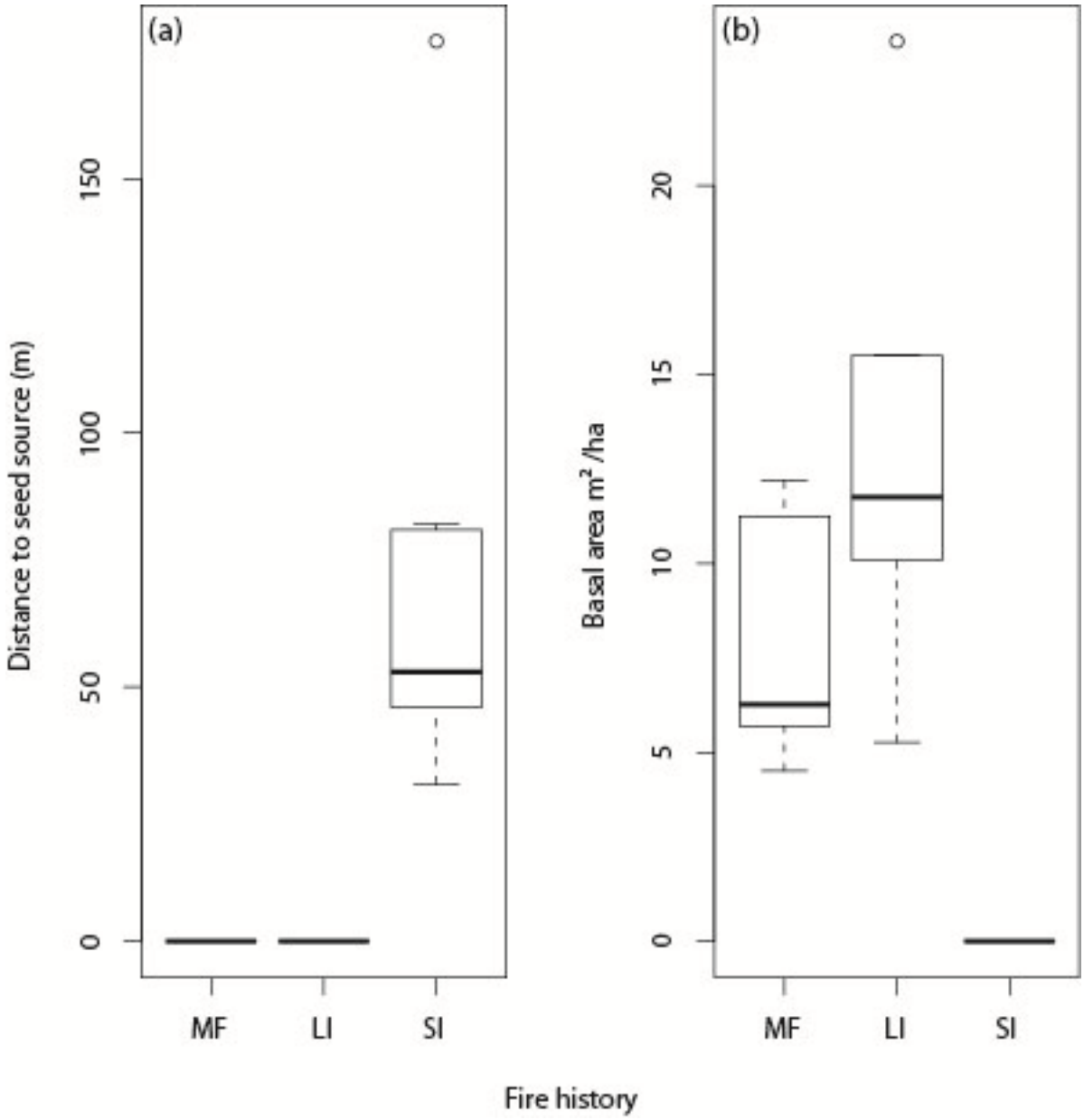

Figure 3-3: Summary of (a) distance to nearest black spruce seed source and (b) basal area, grouped by fire history, where MF=mature forest, LI=long-interval burned, and SI=short-interval burned (n=8 sites per fire history class). Basal area represents fire-killed stems in early successional LI and SI stands and living stems in MF stands.

short periods of establishment on seed beds exposed after fire (Johnson & Fryer, 1989; Johnstone *et al.*, 2004). Secondly, and most importantly for predicting the effects of changing disturbance regimes, historical factors that reduce seed stores and post-fire seed availability can dramatically alter patterns of post-fire stand recruitment and dominance (Lamont *et al.*, 1991; Keeley *et al.*, 1999; Payette *et al.*, 2000; Johnstone & Chapin, 2006b). Because serotinous species depend on onsite seed stores for recruitment (Lamont *et al.*, 1991; Lamont & Enright, 2000), when those stores are limited, they disrupt the feedbacks maintaining the dominance of these species across disturbance intervals.

Natural experiments such as this one provide valuable opportunities for examining ecological responses to large disturbances that are difficult to manipulate directly. However, because fire history treatments were not applied as a true experiment, I must consider other plausible hypotheses for a lack of seed and/or natural seedling germination after two closely timed fires. Black spruce could fail to regenerate after a short fire return interval due to poor seed bed quality, i.e., substrate effects. Seedbed quality has important effects on colonisation after fire in the boreal forest (e.g., Jayen *et al.*, 2006; Johnstone & Chapin, 2006a; Greene *et al.*, 2007). However, SI stands had very low seed availability and very little natural recruitment that was alleviated with the artificial addition of seed, thus we can assume with some confidence that regeneration was limited by seed availability. These responses are consistent with other studies of repeat disturbances that suggest low seed availability may be the cause of recruitment failures or reductions of serotinous species after closely timed disturbances (e.g., Landhausser & Wein, 1993; Tsitsoni, 1997; Keeley *et al.*, 1999; Lloret *et al.*, 2003; Jasinski & Payette, 2005; Johnstone & Chapin, 2006b). In this study, data on both seed availability and recruitment under

natural and artificially increased seed levels allowed me to conclusively demonstrate the role of seed availability in driving these recruitment failures.

The MF stands in this study are more likely candidates for substrate limits on regeneration. These stands have not been burned for more than seventy years (Chapter 5) and have accumulated thick layers of moss and lichen on the forest floor. Previous research has shown recruitment pulses of conifers associated with seed bed availability after disturbance (Johnson & Fryer, 1989; Johnstone *et al.*, 2004; Peters *et al.*, 2005) and that recruitment is reduced on mature forest floor compared to microsites with higher moisture and nutrient availability, such as decomposing logs (Simard *et al.*, 2003; Peters *et al.*, 2006). Where moss and lichen layers remain intact, seedlings are exposed to large fluctuations in temperature and moisture on the porous seed bed (Charron & Greene, 2002; Johnstone & Chapin, 2006a). If a black spruce seed is able to germinate on this type of surface, it is likely to die due to desiccation (Charron & Greene, 2002; Jayen *et al.*, 2006).

Disruption of regeneration pathways reduces the advantage of a serotinous regeneration strategy to favour other strategies, such as long distance dispersal or vegetative resprouting, causing shifts in plant communities (e.g., Johnstone & Chapin, 2006b). I did detect a few black spruce seedlings in SI stands, thus there is potential for them to provide a seed source once they become reproductively mature, allowing for delayed spruce recruitment. However, the data from MF stands show that conifer recruitment is unlikely once the understory has re-established. Thus there are two constraints on succession in SI stands: 1) a lack of available seed for immediate post-fire recruitment; and 2) a seedbed that is inhospitable to spruce seedlings once the few trees that do recruit become reproductively mature. These constraints make serotinous communities

vulnerable to rapid and persistent shifts in stand dominance following two closely timed disturbances (Lamont *et al.*, 1991).

3.4.1 Conclusions

The results of this study provide strong empirical evidence of ecological mechanisms by which changes in fire frequency may lead to rapid shifts in stand dominance in the boreal forest. The vegetation of the boreal forest is thought to be highly resilient to climatic change (Chapin *et al.*, 2004; Chapin *et al.*, 2010), due in part to the adaptations that conifers have that contribute to their self-replacement after fire. This study provides empirical evidence of rapid vegetation change at the northern margin of the boreal forest due to a shortened fire return interval. The indirect climate effects caused by a change to the disturbance regime may initiate vegetation shifts of a larger magnitude or opposite direction than would happen due to climatic change alone. This shift is counter-intuitive to our current predictions regarding climate warming effects on the northern margin of the boreal forest. Instead of the stand in-filling and tree range expansion that is predicted with climatic warming (Kaplan *et al.*, 2003), changes in disturbance regime may initiate the local degradation of treeline forest.

Disturbance is a common occurrence in ecological systems, and recovery from disturbance is a key process structuring ecosystems. For plants, recovery success is strongly influenced by two factors: colonisation and establishment. Here I document that an unusual disturbance event can disrupt strategies selected to ensure the presence of post-fire propagules (serotiny). For species adapted to post-disturbance regeneration, substrate conditions may prevent recruitment in undisturbed conditions. This failure to establish after disturbance can cause long-term disruption because the potential for delayed recruitment is limited by the loss of suitable substrates.

4.0 SEEDBED LIMITATIONS ON TREE RECRUITMENT AFTER SHORT FIRE RETURN INTERVAL

FOREWORD

In the previous chapter, I presented data demonstrating a regeneration failure of black spruce following a short-interval fire. In this chapter, I investigate the relationship between seedbed condition and post-fire regeneration with the goal of predicting the successional trajectory of northern boreal forests based on disturbance history and local environmental factors. This chapter is currently being modified for submission to an ecology journal.

4.1 INTRODUCTION

Fire is the dominant agent of landscape-level vegetation change in the boreal forest (Payette, 1992). Once established, boreal vegetation communities are highly resistant to change (Chapin *et al.*, 2004; Chapin *et al.*, 2010). Fire disrupts these stable communities and initiates processes of secondary succession (Johnson, 1992; Payette, 1992). Typically, northern boreal forests exhibit stand self-replacement after fire (Payette, 1992); however, as climate-disturbance interactions cause changes to historic disturbance regimes, our ability to predict the outcomes of these successional processes may diminish (Sirois & Payette, 1989; Johnstone *et al.*, 2010b; Turner, 2010).

Fire stimulates vegetation change by disrupting boreal forest plant communities through the combustion of biomass on the forest floor and the mortality of the forest canopy (Johnson, 1992; Payette, 1992). The combustion of the forest floor facilitates vegetation change through two processes: 1) the reduction of understory competition via the removal of biomass; and 2) the increase of nutrient availability created by the combustion of biomass and reduction of competition. For some species, fire also facilitates the dispersal of seed from serotinous cones (Lamont *et al.*, 1991). This strategy creates a large influx of seed onto the forest floor in synchrony with the post-fire reduction of competition, contributing to the short period of tree establishment that occurs following a fire (Lamont *et al.*, 1991; Lamont & Enright, 2000; Johnstone *et al.*, 2004; Peters *et al.*, 2005).

Establishment and survival of trees is related to the characteristics of the forest floor substrate, herein referred to as seedbed, after fire. Safe seed sites are microsites, or seedbeds, that are suitable for the germination and establishment of a given species (Harper, 1977; Fowler, 1988; Lamont *et al.*, 1993). As summarized in Chapter 1, soil temperature and moisture, SOH

thickness, and understory competition contribute to the ability of a seed to germinate and survive in a given location (Eriksson & Ehrlen, 1992; Greene *et al.*, 1999). Generally, a newly established seedling requires a consistent source of moisture, suitable temperatures for growth and survival, and access to sunlight, whereas, in the boreal forest, their establishment is negatively correlated to SOH thickness (Charron & Greene, 2002; Purdy *et al.*, 2002; Johnstone & Chapin, 2006a; Hesketh *et al.*, 2009). Moss- and lichen-dominated organic horizons of the boreal forest are poor seedbeds due to the increased drought stress caused by the porous organic surface, which is particularly detrimental to small seeded, deciduous seedlings due to their sensitivity to desiccation (Johnstone & Chapin, 2006a; Greene *et al.*, 2007).

As the climate warms, especially in sub-arctic regions (Chapin *et al.*, 2005), boreal forest fires are predicted to burn larger areas and become more frequent (Balshi *et al.*, 2009; Flannigan *et al.*, 2009). Changes to the fire return interval, or length of time between fires, can alter the structure of the forest floor, where shorter fire return intervals result in shallower SOH due to additive combustion of biomass following two closely timed fires (Chapter 5). If a shortened fire return interval can influence organic horizon thickness, it follows that seedbed characteristics will also be affected and thus the availability of species-specific seedbeds will change. In the absence of seed limitation, the characteristics of the post-fire seedbed will determine the future trajectory of forest succession. Because the individuals that establish in the first few years after fire determine the composition of the mature overstorey, we can use early post-fire recruitment to predict stand successional trajectory (Johnstone *et al.*, 2010b). A shift in successional trajectory from boreal forest cover to, for example, deciduous-dominance will have important implications for ecosystem function and services, such as carbon storage and nutrient cycling.

I have shown that changes in fire frequency can have a direct effect on stand self replacement by influencing seed availability (Chapter 3). Given the potential for additional effects of fire return interval on post-fire regeneration, we need a better understanding of how different fire events can indirectly affect forest recovery by altering stand characteristics such as seedbed quality. My objective was to investigate the relationship between seedbed condition and post-fire tree recruitment. I used experimental tree seedings and plantings in stands of varying fire history to assess seedbed effects on germination, growth, and survival. I hypothesized that black spruce seedbed quality would be highest in stands that were exposed to a typical, long fire return interval of the northwestern boreal forest. Post-fire seedbed composition in a frequently burned stand would provide a more suitable seed bed for upland tree species, i.e., white spruce (*Picea glauca* [Moench] Voss) due in part to warmer and drier soils. I hypothesized that mature forest stands, which have a well developed forest floor, would provide an unsuitable seedbed for all species examined and poor environmental conditions for planted seedling growth. This study experimentally investigates one of the mechanisms, seedbed availability, that dictates post-fire forest composition. Here, I empirically link species establishment and seedbed occurrence patterns to fire history. I do this in a region of overlapping historic fires that act as a case study of predicted future changes in fire frequency. These findings will allow for the use of seedbed composition to predict the successional trajectory of northern boreal stands in a future where unusual fire events are expected to become more frequent.

4.2 METHODS

4.2.1 Study area

This research was conducted in sub-arctic, coniferous forest in the Eagle Plains Ecoregion of Yukon Territory, Canada (66°06’56”N, 137°16’11”W; Figure 3-1). The region is

dominated by black spruce (*Picea mariana* [Mill.] B.S.P.), with occasional white spruce and tamarack (*Larix laricina* [Du Roi] K. Koch) occurring in well-drained habitats. Eagle Plains, an intermontane basin, is characterized by rolling hills with soils composed of fine grain loess over weathered bedrock (Smith *et al.*, 2004). These soils are underlain by continuous permafrost that, in mature forest stands, has <1 m seasonal thaw depth (Tarnocai *et al.*, 1993). The annual freezing and thawing of this layer creates a microtopography of small-scale earth hummocks (Kokelj *et al.*, 2007). Eagle Plains has a continental climate. The monthly summer temperatures during which this study was conducted and 30-year averages of summer temperature and precipitation from the nearest weather stations to the study area (Dawson City, YT; ~290 km SW; 64°02'35"N, 139°07'40"W; and Old Crow, YT; ~190 km NW; 67°34'14"N, 139°50'21"W) are presented in Table 4-1 (Environment Canada, 2011). Although these data do not summarize the climate of the study area, they do represent the regional trends of each field season.

The recent fire history of Eagle Plains allowed for the sampling of a mosaic of stands of varying fire return interval. Two fires with similar characteristics and behaviour burned adjacent stands of black spruce in 1990 (33,500 ha) and 1991 (4,800 ha; see Chapters 3 and 5 for further details). In 2005, a third fire occurred in the vicinity (69,000 ha), partially overlapping areas that had been burned in the 1990 and 1991 fires. This fire history allowed me to establish my field experiment in stands that had experienced a long fire return interval (LI; burned in 2005 after ~94 year fire return interval), short fire return interval (SI; burned in 1990/91 and 2005), and within stands that had not been burned for several decades (mature forest; MF; last fire ~77 years before sampling).

Table H: Summer monthly and 30-year average (with standard deviation) temperature and precipitation and number of frost free days (minimum temperature >0°C; May to August) at Old Crow and Dawson City, YT (n/a=data not available; Environment Canada, 2011).

		Old Crow						Dawson City					
		May	June	July	August	Summer	Frost free days	May	June	July	August	Summer	Frost free days
Temperature	2007	1.4	14.3	16.2	11.8	10.9	104	9.1	15.6	16.9	14.9	14.1	108
(°C)	2008	3.6	15.1	14.1	7.7	10.1	102	8.7	16	14.6	11.4	12.7	108
	2009	5.2	12.9	14.5	8.7	10.3	95	8.5	16	18.2	12.9	13.9	109
	2010	7.6	13.9	15.4	13	12.5	111	11.7	15.5	16.6	14.5	14.6	112
30-year average		2.5	12.4	14.6	10.9	10.1	94	8.3	13.7	15.6	12.5	12.5	104
		(2.7)	(1.3)	(1.4)	(1.9)			(1.3)	(1.1)	(0.8)	(1.4)		
Precipitation	2007	24	32.7	24.2	27.9			n/a	14	53.7	n/a		
(mm)	2008	18.8	25.8	n/a	n/a			15.8	n/a	n/a	n/a		
	2009	n/a	n/a	n/a	n/a			n/a	n/a	n/a	n/a		
	2010	n/a	n/a	n/a	n/a			n/a	n/a	n/a	n/a		
30-year average		14.7	36.4	36	46.4			28.4	40.4	48.4	42.5		

4.2.2 Field measurements

In 2007, eight experimental sites were placed within each of the three fire histories (MF, LI, and SI stands, for a total of 24 experimental sites). Sites were placed in an attempt to capture the natural variation in the study area. MF and LI stands had similar tree density, although differed in basal area (see Chapter 5 for further stand characteristics). Each site consisted of seeded plots and planted seedlings (Figure 4-1).

4.2.2.1 Seeded plots

Ten blocks of seeded plots were positioned within each experimental site. Each complex consisted of six 0.5 m x 0.5 m plots. The complexes were stratified by microtopography, with half located on earth hummocks and half in hollows (n=5/microtopography). There was no detectable difference in the distribution of hummock-hollow microtopography between fire history classes (Chapter 5). I selected four tree species native to the northwestern boreal forest of North America for seeding: black spruce (seed from Tok, AK; ~63°19'N, ~142°58'W), white spruce (seed from 64°09'37"N, 138°32'54"W), Alaskan birch (*Betula neoalaskana* Sargent; seed from Fairbanks, AK; 64° 51' 24"N, 147° 48' 10"W), and balsam poplar (*Populus balsamifera* L; seed from Dawson City, YT; 64°3'N, 139°24'W). Trembling aspen (*Populus tremuloides* Michaux) seed production was very low during the study period, and I was unable to collect sufficient seed to use in the experiment. Balsam poplar was selected as a suitable substitute due to the similarity in germination requirements to trembling aspen and widespread distribution in the general area (Zasada *et al.*, 1992). The fifth plot in each complex was seeded with black spruce in 2008, the results of which are discussed in Chapter 3.

Seed was evenly spread across the seeded plots by hand. Seeds were applied to the plots according to the natural timing of dispersal for that species (Table 4-2). For example, black

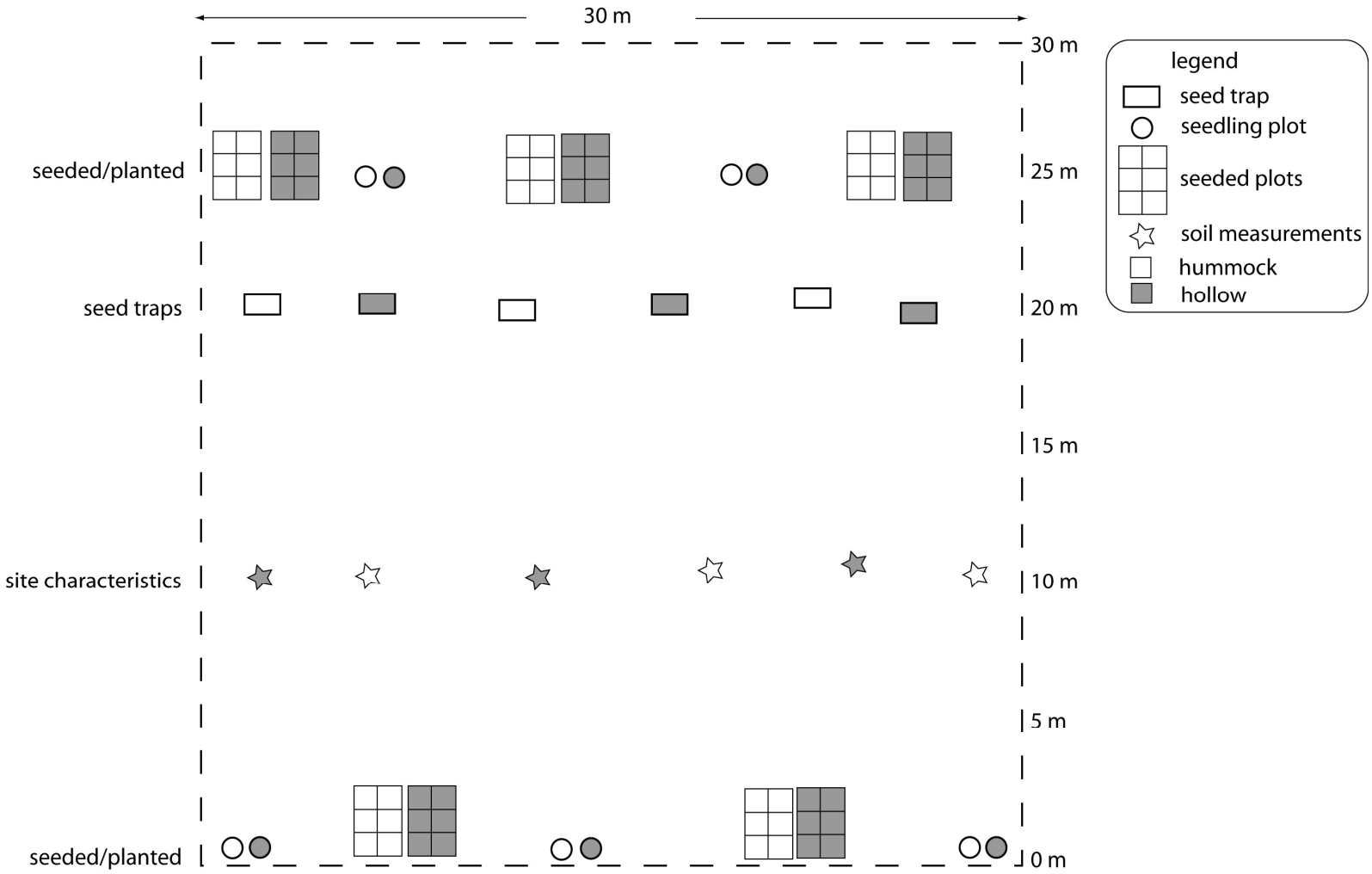

Figure 4-1: Schematic of experimental site configuration.

Table I: Date of experimental seedings for each species tested.

Species	Date of seeding	Seed mass/plot (g)	Seeds/plot
black spruce	August 2007	~0.3	~250
white spruce	June and August 2007	~0.5	~250
Alaskan birch	June and August 2007	~0.03	~100
balsam poplar	July 2008*	~0.01	~75

*when regional seed was mature

spruce seeds were sown in late summer to allow for winter stratification. White spruce and Alaskan birch naturally disperse in the fall and winter (Zasada *et al.*, 1992), but I applied their seeds in spring and fall to maximize the number of plots seeded with these two species. The sixth plot in each complex was left unseeded for measurements of natural recruitment of trees in each site (see Chapter 3). Emerged seedlings were counted in each plot in June, July, and August in 2008 and 2009, and in July 2010. This frequency of observation allowed me to distinguish between newly emerged individuals and older recruits. In August 2009, the seedling count included recording the substrate from which each seedling had emerged, based on the 12 substrates classes described below. Substrate association was recorded separately for each species surveyed.

I determined the substrate composition of each seeded plot by measuring the percent cover of 12 substrate classes (Table 4-3) in July, 2009. Substrate was defined as the ground layer or seedbed on which dispersed seed was likely to land. A substrate that was present in a plot but did not occupy measurable cover was assigned a percent cover of 1. Substrate covers between 'present' and 5% were measured in increments of 1%. All covers 5% or greater were measured in increments of 5%.

4.2.2.2 Planted seedlings

Ten blocks of native tree seedlings were planted within each site in June, 2008. Each complex contained two black spruce seedlings and one seedling each of white spruce, Alaskan birch, and trembling aspen. Seed for each species was collected from a northwestern boreal forest population. Both seedlings of black spruce were grown from two separate populations of seed collected in August, 2007. 'Tombstone' black spruce originated from a stand just south of Tombstone Territorial Park, Yukon (64^{o}09'37"N, 138^{o}32'54"W), which is located in continuous

Table J: Substrate classes observed in the study area. The proportion of each substrate is indicated for each fire history class (mean of n=8 sites/fire history class). MF=mature forest; LI=long-interval burn; SI=short-interval burn. The percentage of seedlings germinated on each substrate is indicated, with the raw count of seedlings that emerged in parentheses.

		Fire history class			Species		
Substrate	Description	MF	LI	SI	black spruce	white spruce	Alaskan birch
colonizer moss	*Ceratadon*-type mosses	0	28.3	39.1	66.6 (1380)	52.6 (111)	67.1 (102)
plant litter	dead plant debris that prevented seed access to substrate below	8.7	14.1	27.8	7.3 (151)	14.7 (31)	8.6 (13)
mineral soil	exposed mineral soil	0	1.8	13.9	1.2 (38)	3.3 (7)	5.9 (9)
charred moss	burnt organic layers	0	47.3	9.6	10.4 (215)	15.6 (33)	10.5 (16)
Polytrichum	*Polytrichum* spp. (e.g., *P. juniperinum*)	0.2	4.8	5.6	4.2 (88)	1.9 (4)	2.6 (4)
rock	exposed rock	0	0	1.9	0	0	0
Marchantia	*Marchantia polymorpha*	0	3	1.8	3.5 (72)	3.8 (8)	3.3 (5)
lichen	grouping of all lichen sp.	30.9	0.2	0.3	0.0004 (1)	0	0
Sphagnum	*Sphagnum* sp. moss	24.8	0.1	0	5 (105)	5.2 (11)	0
pleurocarpous moss	prostrate, branched mosses (e.g., *Hylocomium splendens*)	23.1	0	0	0.1 (3)	1.4 (3)	2 (3)
acrocarpous moss	erect, rarely branched mosses (e.g., *Dicranum* spp.)	10.3	0	0	0.9 (18)	1.4 (3)	0
brown moss	desiccated moss cover of any sp.	1.8	0	0	0	0	0

boreal forest well south of the treeline. ‘Eagle’ black spruce originated from within the study area (65°57’24”N, 137°21’34”W). White spruce seed was collected from a stand ~5 km south of the Tombstone black spruce stand. The trembling aspen and birch seedlings were grown from seed collected in Fairbanks, Alaska (64° 51' 24"N, 147° 48' 10"W). There was not a sufficient quantity of trembling aspen to use for both the seedlings and seeded plots, as described above. Seedlings were grown in controlled conditions in Saskatchewan prior to their transport to the study area. Conifer seedlings were grown in peat moss in order to simulate the natural acidic properties of coniferous stands. Deciduous seedlings were grown in an equal mix of peat moss, perlite, and ProMix potting mixture. No fertilizer was used during seedling propagation. The conifer seedlings were grown in 19 hours of light per day. The Eagle population seed originated from a latitude just south of the Arctic Circle, thus receiving 24 hours of sunlight at the peak of summer. Under greenhouse conditions, the Eagle Plains population was stimulated to stop accumulating biomass and to set bud. This resulted in the Eagle seedlings being smaller than the Tombstone seedlings at the time of planting, making comparisons between the two populations more difficult.

Seedlings were planted in the same arrangement in each plot for easy species identification. Seedling height, basal diameter, and health were measured in August, 2008, June, July, and August, 2009, and in July, 2010. Health was assessed as ‘good’ or ‘poor’. Yellow or brown seedlings were designated as being in ‘poor’ condition. Any signs of herbivory, dieback, or other damage were recorded. These observations helped me to determine the cause of death for those seedlings that did not survive for the entire experimental period. After the final measurements in July, 2010 I collected the aboveground biomass of each seedling by clipping each individual at ground level. Aboveground biomass was oven-dried at 30° C for 48 hours.

Leaf and stem tissues of each seedling were separated by hand and weighed individually to 0.001 g.

4.2.2.3 Environmental characteristics

SOH thickness, temperature, moisture, and depth of thaw were measured on earth hummocks and in hollows along a 30 m east-west transect within each study site. Three hummocks and three hollows were randomly selected along the sampling transect in each study site, for a total of six measurements of each variable per site. At each sample point I measured the thickness of the SOH from the top of the green moss layer of the forest floor to the mineral soil surface. Soil temperature was measured using a hand-held digital thermometer in the top 5 cm of the mineral soil. Soil moisture was measured in the top 5 cm of the mineral soil using ECH_2O EC-TM soil moisture probe read by an Em50 data logger (Decagon Devices Inc., Pullman, WA, U.S.A.). SOH thickness, soil temperature, and soil moisture were measured once in July 2009. Trends in soil moisture and temperature presented below were consistent with repeated measurements of these variables, regardless of the timing of measurement. Depth of thaw (cm) was measured with a probe in five hummocks and five hollows along the same transect in August 2008. When the depth of thaw exceeded the length of the probe, depth was recorded as >1.2 m (probe length). I averaged each variable to obtain a single mean value for each site.

4.2.3 Statistical analyses

4.2.3.1 Seeded plots

All seedlings that emerged within a seeded plot, whether or not they survived, were summed to calculate total emergence. Counts from the seeded plots were summed in each site for

the six groups of species seeded: fall-seeded black spruce, spring-seeded white spruce, fall-seeded white spruce, spring-seeded birch, fall-seeded birch, and balsam poplar.

I used the unseeded control plots as a baseline for natural recruitment in the three fire history classes and to identify the naturally recruiting species in the area. In Chapter 3, I subtracted the number of black spruce in control plots from those growing in seeded plots to isolate the effect of seed application. Alaskan birch was detected in some of the control plots, thus data from birch seeded plots was corrected in the same manner as black spruce. Here, I used the corrected black spruce emergence results from Chapter 3 to compare black spruce recruitment patterns to those of white spruce, Alaskan birch, and balsam poplar.

I used count data for all analyses of emergence in seeded plots. The structure of count data, which has no negative values, required that I first analyze the data using generalised linear models (GLMs) with Poisson distributions, incorporating the natural logarithm as the link function (Zuur *et al.*, 2009). All models were overdispersed (residual deviance/residual degrees of freedom > 1). To account for the overdispersion, all models were adjusted to use a negative binomial distribution rather than Poisson. For each pair of models, I used a likelihood ratios test to confirm that the negative binomial GLM provided a better model fit (Zuur *et al.*, 2009). In each model, the intercept represented expected seedling counts in LI stands and hollows.

4.2.3.2 Planted seedlings

I used GLMs to compare planted seedling survival of each species using fire history and microtopography as predictor variables. I defined seedling survival as the number of live seedlings in July 2010. Because the number of surviving seedlings is categorized as count data, I used GLMs with Poisson distributions, incorporating the natural logarithm as the link function

(Zuur *et al.*, 2009). In each model, the intercept represented expected seedling counts in LI stands and hollows.

I explored patterns of mortality by investigating the relationship between cause of death, species, and fire history. Cause of death was summarized into four categories: animal (herbivory or trampling), winter death, environment (desiccation), and human (transplantation or mortality during basal diameter measurement). The number of deaths in each category was summed for each species at the site level. The site-level data were analyzed using GLMs with Poisson distributions with each cause of death analyzed in a separate model and species and fire history as response variables. Eagle black spruce survival was related to seedling height at the time of planting using a GLM with binomial distribution. In each model, the intercept represented expected seedling counts of Alaskan birch and LI stands.

I compared growth of all species planted using multivariate analysis of covariance (MANCOVA) with Pillai's Trace test statistic (Scheiner, 1993). Pillai's Trace tests the null hypothesis that the group means of the response variables are equal. The response variables included seedling height, basal diameter, and aboveground biomass as measured in July, 2010. The MANCOVA included species, fire history (MF, LI, SI) and microtopography (hummock, hollow) as categorical predictor variables. I included initial seedling height, measured in July 2008, as a covariate to help remove the effect of original seedling size, which may have been influenced by small-scale variations in greenhouse conditions. This analysis was conducted using those individuals that survived to the end of the experimental period. Some seedlings had negative growth values over the experimental period due to herbivory, trampling, or winter dieback, but were still included in the analyses. I followed the significant MANCOVA with an

ANCOVA for each response variable, with initial seedling size, species, fire history, and microtopography as predictor variables.

4.2.3.3 Seedbed

Using contingency tables, I compared the observed number of emergent seedlings of each species on each substrate to the number of emergent seedlings we expected based on the availability of substrates. My null hypothesis was that seedling emergence was evenly distributed across all substrates. I calculated the expected number of emergents for each species by first calculating the mean proportion of cover for each substrate in each fire history class (12 substrates x 8 sites x 3 fire history classes). I then multiplied the mean proportion of cover per site by the mean number of emergent seedlings observed per site. This value gave me the number of emergent seedlings that I would expect to find on each substrate, based on the proportion of each site that the substrate occupied. I calculated a χ^2 statistic for each site by comparing the expected counts to the observed counts, testing the null hypothesis that there was no difference between expected and observed counts. This procedure was conducted for black spruce, white spruce, and Alaskan birch separately. I explored the relationship between soil moisture and colonizer moss cover and colonizer moss cover and black spruce, white spruce, and Alaskan birch cover using Pearson's product-moment correlations (Crawley, 2007).

SOH thickness, soil moisture, soil temperature, and depth of thaw were examined using four separate two-way ANOVAs, each with fire history classes and microtopography as predictor variables. I explored the relationship between SOH thickness and soil temperature, SOH thickness and soil moisture, and soil temperature and soil moisture using Pearson's product-moment correlation (Crawley, 2007).

For all models, I assessed model fit using residual diagnostics (Zuur *et al.*, 2009). All statistical analyses were conducted with R (R Development Core Team, 2009) using the "MASS" package for negative binomial GLMs (Venables & Ripley, 2002).

4.3 RESULTS

4.3.1 Seedling emergence and growth

4.3.1.1 Seeded plots

Regardless of species or time of seeding more seedlings emerged in hollows than on earth hummocks (Figure 4-2, Table 4-4). Seedling emergence of all species was consistently lowest in mature forest stands. Standardizing seedling emergence to mass of seeds sown showed that black spruce > Alaskan birch > white spruce emergence (Figure 4-2).

Spring-seeded Alaskan birch (Figure 4-2a) was the only experimental seeding with significant interactions in a GLM. Spring birch emergence was significantly influenced by the interaction between fire history and soil moisture, where birch emergence increased with soil moisture in SI stands (Table 4-4). There was also a significant interaction between microtopography and soil moisture, where birch emergence increased with soil moisture on earth hummocks. Birch emergence was lowest in mature forest stands and on hummocks.

Fall-seeded Alaskan birch (Figure 4-2b), spring-seeded white spruce (Figure 4-2c) and fall-seeded white spruce (Figure 4-2d) showed similar patterns of emergence (Table 4-4). There were no significant effects of interactions between fire, microtopography, or soil moisture on any of these species. In all three models, mature forest stands and hummocks had the lowest black spruce emergence, and there was no significant effect of soil moisture (Table 4-4).

The responses of the black spruce seeding experiment are presented in detail in Chapter 3. I showed that black spruce emerged well in LI and SI stands when seeded, but had little

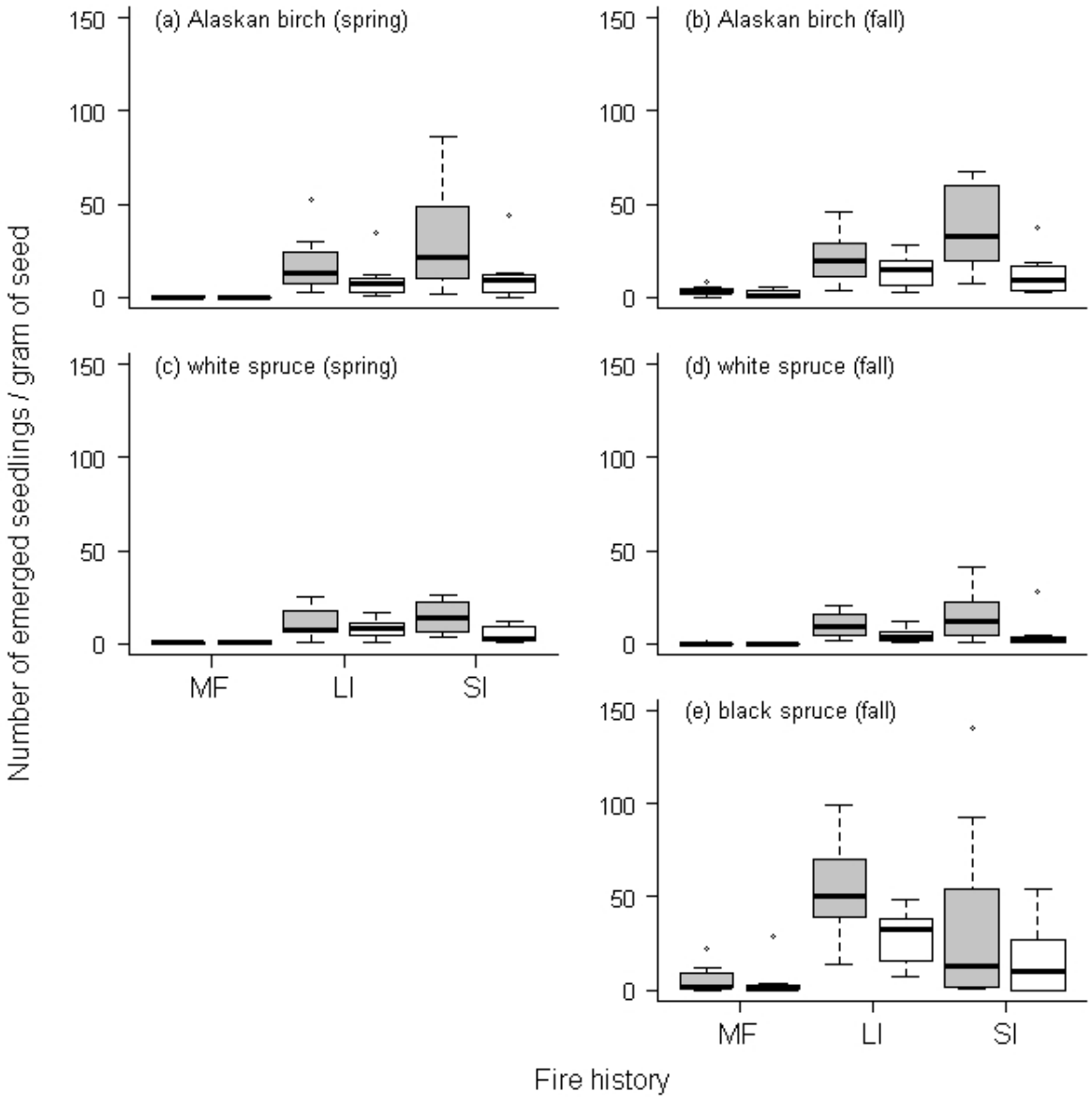

Figure 4-2: Number of seedlings that emerged per gram of seed, grouped by species, fire history, and microtopography. Different panels show Alaskan birch seeded in (a) spring and (b) fall, white spruce seeded in (c) spring and (d) fall, and (e) black spruce seeded in fall. Fire history classes are: MF=mature forest, LI=long-interval burned, and SI=short-interval burned (n=8 sites/fire history class with 1.25 m^2 sampled for each seed treatment-microtopography combination in each site). Box colour indicates microtopography: plots were located on earth hummocks (white) and in hollows (grey).

Table K: Negative binomial generalised linear models of total seedling emergence for spring- and fall-seeded Alaskan birch and white spruce. Bolded model terms indicate the response variable for each model. All models included fire history class, microtopography, and soil moisture as predictor variables. The intercept represents expected seedling counts in LI stands and hollows. Bolded z-values indicate that a significant difference ($\alpha \leq 0.05$) was detected in the model.

Model term	Estimate	Standard error	z-value	Model term	Estimate	Standard error	z-value
Alaskan birch (spring)				**white spruce (spring)**			
Intercept	5.110	1.121	**4.558**	Intercept	4.1862	0.5120	**8.176**
SI	-2.769	1.501	-1.845*	SI	-0.3519	0.3092	-1.138
MF	-7.603	3.363	**-2.261**	MF	-2.5362	0.3714	**-6.829**
hummock[1]	-3.744	1.457	**-2.570**	hummock	-0.7652	0.2934	**-2.608**
soil moisture	-4.874	2.425	**-2.010**	soil moisture	-1.6538	0.9702	-1.705**
SI*hummock	2.032	1.111	1.829*				
SI*soil moisture	9.351	4.144	**2.256**				
hummock*soil moisture	8.170	3.578	**2.283**				
Alaskan birch (fall)				**white spruce (fall)**			
Intercept	3.7661	0.4574	**8.234**	Intercept	3.1804	0.7960	**3.996**
SI	0.1249	0.2899	0.431	SI	0.3032	0.4360	0.696
MF	-1.7758	0.3287	**-5.403**	MF	-5.1644	0.9056	**-5.703**
hummock	-0.8511	0.2757	**-3.087**	hummock	-0.9289	0.4011	**-2.316**
soil moisture	-0.6552	0.8335	-0.786	soil moisture	0.3543	1.6124	0.220

[1]Plots located on hummock microtopography
*p=0.07 **p=0.09

recruitment in mature forest stands. More black spruce seedlings emerged in hollows than on earth hummocks (Figure 4-2e). Plots with the most black spruce occurred in hollows in LI stands.

Balsam poplar seedlings did not emerge in any of the plots and thus were not included in the graphical results. I tested the viability of the balsam poplar seed used in this field experiment prior to planting, and found it to be sufficiently viable (three viability trials resulted in 69, 79, and 79% viability).

4.3.1.2 Planted seedlings: survival

Fire history and microtopography did not affect the survival of conifer seedlings (Table 4-5, Figure 4-3). However, the deciduous species' survival was affected by fire history. There was a significant effect of the interaction between fire history and microtopography on trembling aspen survival. Hummocks in mature forests supported significantly fewer surviving trembling aspen (Table 4-5); however, mature forests had higher survival of trembling aspen than LI and SI stands ($z=2.12$, $p=0.03$), and more aspen survived on hummocks than hollows ($z=2.58$, $p=0.01$). MF stands also had more Alaskan birch ($z=2.53$, $p=0.01$) than LI and SI stands. There was no effect of microtopography on birch survival. I also detected a difference in survival between species. White spruce had the highest ($z=11.08$, $p<0.0001$) and Eagle Plains black spruce the lowest survival ($z=-2.95$, $p=0.003$) of all seedlings.

Of the 1200 seedlings planted, 31 died due to human error, 126 due to animal, 126 due to environmental conditions, and 146 died over the winter, i.e., between the August and June surveys. More seedling deaths were animal-caused in LI and SI stands than MF stands (Table 4-6) and more trembling aspen and birch died due to animals than did conifers. Snowshoe hare (*Lepus americanus*) and tundra vole (*Microtus oeconomus*) were the most common herbivores

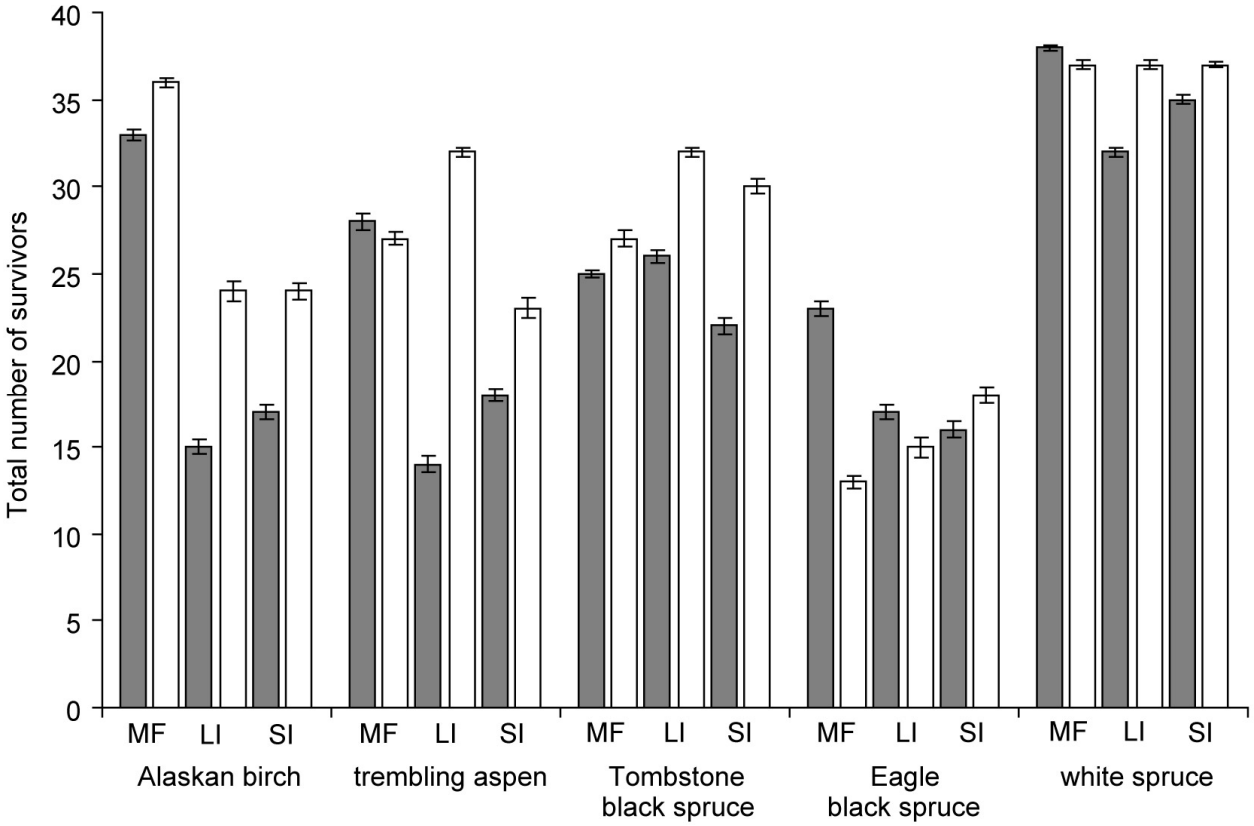

Figure 4-3: Total number of surviving seedlings of each tree species planted, grouped by fire history (MF=mature forest; LI=long-interval burned stand; SI=short-interval burned stand) and microtopography (grey=hollow, white=earth hummock). The maximum number of surviving seedlings per category (bar) is 40.

Table L: Summary of results from the Poisson generalised linear models of survival for each of group of planted seedlings. The bolded species name indicates the seedlings modelled. All models included fire history and microtopography as predictor variables. The intercepts represent expected seedling counts in LI stands and hollows. Bolded p-values indicate a significant difference ($\alpha \leq 0.05$) in the model.

Model term	Estimate	Standard error	z-value	Model term	Estimate	Standard error	z-value
Alaskan birch				**trembling aspen**			
Intercept	0.6286	0.2582	**2.435**	Intercept	0.5596	0.2673	**2.094**
SI	0.1252	0.3542	0.353	SI	0.2513	0.3563	0.705
MF	0.7885	0.3114	**2.532**	MF	0.6931	0.3273	**2.118**
hummock[1]	0.4700	0.3291	1.428	hummock	0.8267	0.3204	**2.580**
SI*hummock	-0.1252	0.4570	-0.274	SI*hummock	-0.5816	0.4491	-1.295
MF*hummock	-0.3830	0.4079	-0.939	MF*hummock	-0.8630	0.4188	**-2.061**
Tombstone black spruce				**Eagle black spruce**			
Intercept	1.17865	0.19612	**6.010**	Intercept	0.75377	0.24254	**3.108**
SI	-0.16705	0.28968	-0.577	SI	-0.06062	0.34832	-0.174
MF	-0.03922	0.28011	-0.140	MF	0.30228	0.31985	0.945
hummock	0.20764	0.26403	0.786	hummock	-0.12516	0.35425	-0.353
SI*hummock	0.10252	0.38536	0.266	SI*hummock	0.24295	0.49350	0.492
MF*hummock	-0.13068	0.38308	-0.341	MF*hummock	-0.44538	0.49587	-0.898
white spruce							
Intercept	1.38629	0.17678	**7.842**				
SI	0.08961	0.24458	0.366				
MF	0.17185	0.23993	0.716				
hummock	0.14518	0.24141	0.601				
SI*hummock	-0.08961	0.33745	-0.266				
MF*hummock	-0.17185	0.33410	-0.514				

Table M: Summary of results from the Poisson generalised linear models of seedling death. I modelled the number of species that succumbed to each cause of death separately, with species and fire history class as predictor variables. The intercepts represent expected seedling counts of Alaskan birch and LI stands. Bolded z-values indicate that a significant difference ($\alpha \leq 0.05$) was detected in the model.

Model term	Estimate	Standard error	z-value	Model term	Estimate	Standard error	z-value
Animal				**Environment**			
Intercept	0.6381	0.1967	**3.243**	Intercept	-0.6657	0.3009	**-2.213**
black spruce (Eagle)	-0.8109	0.3005	**-2.699**	black spruce (Eagle)	1.368	0.2993	**4.571**
trembling aspen	0.5436	0.2095	**2.594**	trembling aspen	7.618×10^{-9}	0.3779	2.02×10^{-8}
black spruce (Tomb)	-1.5041	0.3909	**-3.848**	black spruce (Tomb)	0.8267	0.3204	**2.580**
white spruce	-2.1972	0.5270	**-4.169**	white spruce	-0.2412	0.4029	-0.599
SI	-0.1636	0.2027	-0.807	SI	-0.1452	0.2414	-0.601
MF	-0.6381	0.2336	**-2.731**	MF	0.4321	0.2111	**2.047**
Winter-kill				**Human error**			
Intercept	0.50636	0.20027	**2.528**	Intercept	-1.4346	0.5430	**-2.642**
black spruce (Eagle)	0.53408	0.21599	**2.473**	black spruce (Eagle)	0.3939	0.5900	0.668
trembling aspen	-1.04145	0.33577	**-3.102**	trembling aspen	0.3980	0.5897	0.675
black spruce (Tomb)	-0.02985	0.24437	-0.122	black spruce (Tomb)	-0.2870	0.6700	-0.428
white spruce	-1.32914	0.37485	**-3.546**	SI	0.7612	0.4679	1.627
SI	0.11583	0.18212	0.636	MF	-1.1120	0.7108	-1.564
MF	-0.82418	0.23988	**-3.436**				

depredating on deciduous seedlings (C. Brown, personal observation). More seedling deaths were caused by environmental conditions in MF than LI or SI stands. The two populations of black spruce had significantly more deaths due to environmental conditions, primarily desiccation, than the deciduous species or white spruce. Seedling deaths over the winter occurred more in MF stands than burned stands and the majority of them were Eagle black spruce. Surviving Eagle black spruce were taller at time of planting than those that died ($z=-4.59$, $df=239$, $p<0.0001$). There was no pattern detected in seedlings killed due to human error between species or fire history classes.

4.3.1.3 Planted seedlings: growth and biomass

Species and fire history interacted to have a significant effect on seedling growth over the experimental period, indicated by MANCOVA (Pillai=0.14, df=8, approximate $F=4.41$, $p<0.0001$). Initial seedling height had significant interactions with species (Pillai=0.12, df=4, approximate $F=7.2$, $p<0.0001$), fire history (Pillai=0.06, df=2, approximate $F=7.14$, $p<0.0001$), and microtopography (Pillai=0.01, df=1, approximate $F=2.92$, $p=0.03$). Species (white spruce>Alaskan birch>Tombstone black spruce>Eagle black spruce=trembling aspen; Pillai=0.29, df=4, approximate $F=18.46$, $p<0.0001$) and fire history (SI>LI>MF; Pillai=0.24, df=2, approximate $F=31.03$, $p<0.0001$) had significant main effects on growth, whereas microtopography did not (Pillai=0.004, df=1, approximate $F=0.42$, $p=42$). Growth was greatest for white spruce on hummocks in SI stands.

Separate MANCOVAs for each species indicated that for all populations planted, fire history had a significant effect on seedling growth (e.g., Figure 4-4; Table 4-7). Seedlings planted in SI stands had taller, thicker stems and more biomass than other sites. The effect of

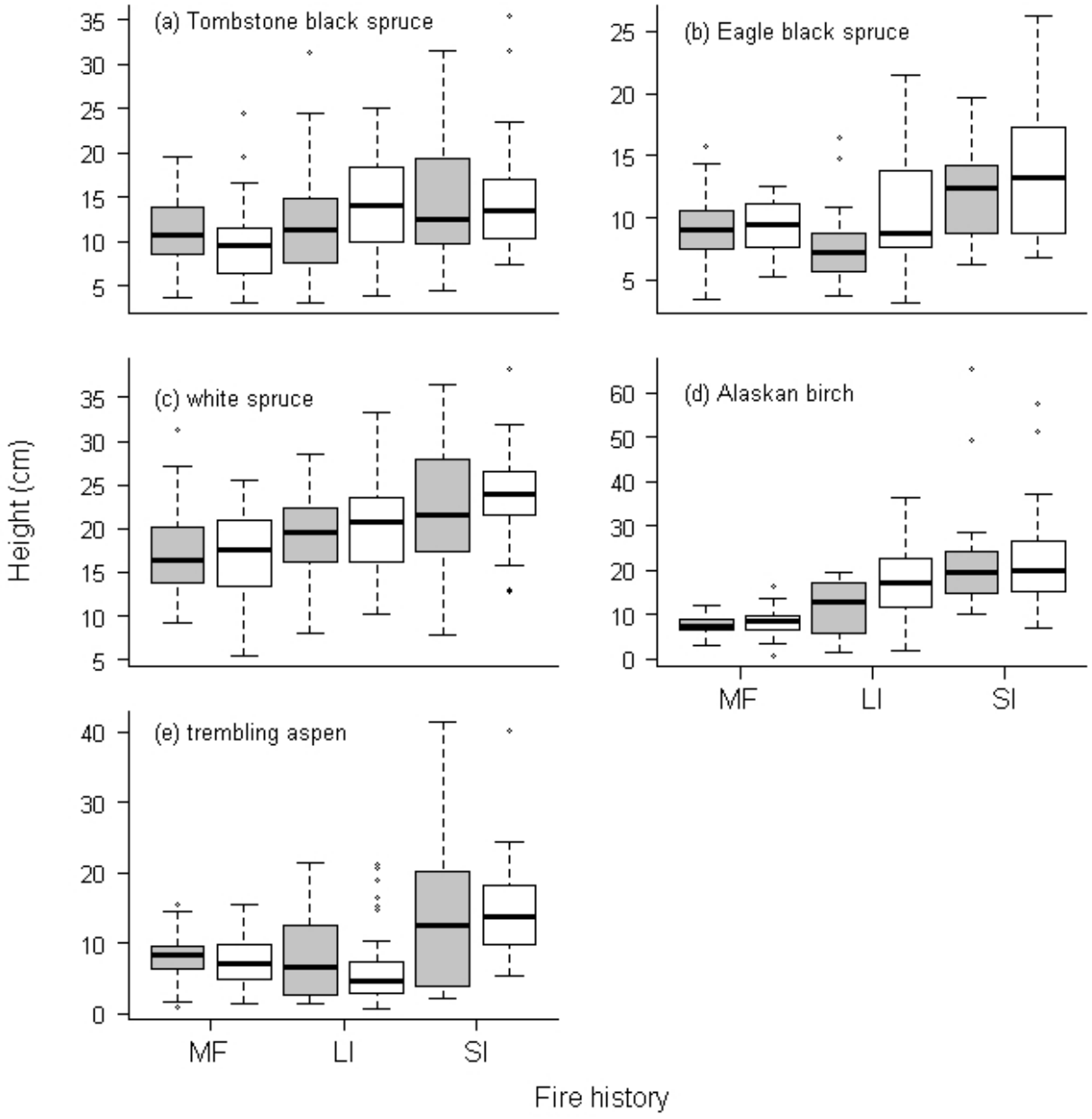

Figure 4-4: Total height (cm) of (a) Tombstone black spruce, (b) Eagle black spruce, (c) white spruce, (d) Alaskan birch, and (e) trembling aspen measured in July 2010. Fire history classes are: MF=mature forest, LI=long-interval burned, and SI=short-interval burned (n=8 sites/fire history class). Box colour indicates microtopography: plots were located on earth hummocks (white) and in hollows (grey).

Table N: Summary of results from the multivariate analysis of variance for each of the groups of planted seedlings. The bolded species name indicates the seedlings modelled. The response variables included seedling height increase, basal diameter increase, and aboveground biomass. All models included fire history and microtopography as predictor variables. Bolded p-values indicate a significant difference ($\alpha \leq 0.05$) between groups was detected in the model.

	df	Pillai	p-value
Trembling aspen			
fire	2	0.2478	**<0.0001**
microtopography	1	0.0248	0.34
fire*micro	2	0.0465	0.38
Alaskan birch			
fire	2	0.4098	**<0.0001**
microtopography	1	0.0134	0.60
fire*micro	2	0.0481	0.34
White spruce			
fire	2	0.2605	**<0.0001**
microtopography	1	0.0503	**0.014**
fire*micro	2	0.0167	0.75
Tombstone black spruce			
fire	2	0.1428	**0.0009**
microtopography	1	0.0117	0.62
fire*micro	2	0.0344	0.50
Eagle black spruce			
fire	2	0.2091	**0.002**
microtopography	1	0.0739	0.06
fire*micro	2	0.0447	0.63

microtopography on seedling growth was mixed; birch, aspen, and Tombstone black spruce showed no effect of microtopography, whereas white spruce and Eagle black spruce did.

ANCOVAs for trembling aspen seedling growth indicated that aspen in SI stands were taller than LI and MF stands ($p<0.0001$ and $p<0.0001$, respectively) and had thicker stems than LI stands ($p=0.02$), but not MF stands ($p=0.08$). Aspen biomass was greater in SI stands then LI ($p=0.002$) and MF stands ($p<0.0001$). Patterns in Alaskan birch seedling growth were very similar to trembling aspen. Birch seedlings grown in SI stands were taller ($p<0.0001$ and $p<0.0001$), had thicker stems ($p=0.004$ and $p<0.0001$), and greater biomass ($p=0.002$ and $p<0.0001$) than LI and MF stands, respectively (Figure 4-4). LI stands had taller ($p=0.0008$) and thicker ($p=0.0001$) stems and greater biomass ($p=0.03$) than MF stands. There was no effect of microtopography on growth in either deciduous species.

White spruce seedling height decreased with SI>LI>MF stands (SI-LI: $p=0.01$; SI-MF: $p<0.0001$; MF-LI: $p<0.0001$), whereas stem basal diameter was not influenced by fire history. White spruce biomass was greater in SI stands than LI ($p=0.02$) and MF stands ($p<0.0001$). White spruce growth differed significantly between microtopography (Table 4-7), where seedling stems were taller and thinner on earth hummocks than in hollows. There was no effect of fire history or microtopography on white spruce biomass.

The two black spruce populations had a similar growth response to fire history, but differed in their response to microtopography (Figure 4-4). Tombstone black spruce were taller in SI stands than LI ($p=0.02$) and MF ($p=0.0005$) stands and had thicker stems in SI ($p=0.007$) and LI ($p=0.03$) stands than MF stands. Biomass was significantly less in MF stands than LI stands ($p=0.02$). We did not detect a microtopography effect in Tombstone black spruce growth. Eagle black spruce were taller and had greater biomass in SI stands than LI ($p=0.05$ and

p=0.003) and MF (p=0.003 and p<0.0001) stands, respectively, and had thicker stems in SI stands than MF stands (p=0.02). In contrast to Tombstone black spruce, Eagle black spruce growth differed significantly between microtopography classes at the α=0.06 level. Seedling stems were taller (p=0.04), thicker (p=0.04), and had more biomass (p=0.02) on earth hummocks than hollows.

4.3.2 Seedbed effects

Substrates were assigned to 12 substrate classes within the three fire history classes (Table 4-3). Contingency tables of observed versus expected frequencies of emergent seedlings indicated that the seedling emergence was not equivalent across all substrates. I highlight the most relevant to post-fire regeneration here: colonizer moss, charred moss, and Sphagnum moss substrates, which are the most common substrates in the study area. There were very few emergent seedlings of any species on the other substrates, including mineral soil (Table 4-3).

The number of black spruce emergents on colonizer moss substrate was greater than expected in LI and SI stands (χ^2=1219, p<0.0001; χ^2=2369, p<0.0001, respectively). In LI stands, the greater-than-expected emergence occurred on hummocks and in hollows, whereas in SI stands, black spruce emergence was less than expected on earth hummocks, but greater than expected in hollows (Figures 4-5 and 4-6). This pattern of lower than expected emergence on colonizer moss on hummocks and higher than expected emergence in hollows was also observed for white spruce (LI: χ^2=311, p<0.0001; SI: χ^2=486, p<0.0001) and Alaskan birch (LI: χ^2=853, p<0.0001; SI: χ^2=1341, p<0.0001) emergents. The emergence of all species was significantly less than expected on charred moss in SI stands (black spruce: χ^2=56, p<0.0001; white spruce: χ^2=27.6, p=0.02; Alaskan birch: χ^2=45, p<0.0001). Although there was a greater proportion of substrate composed of charred moss in LI stands, there was still very little emergence of any

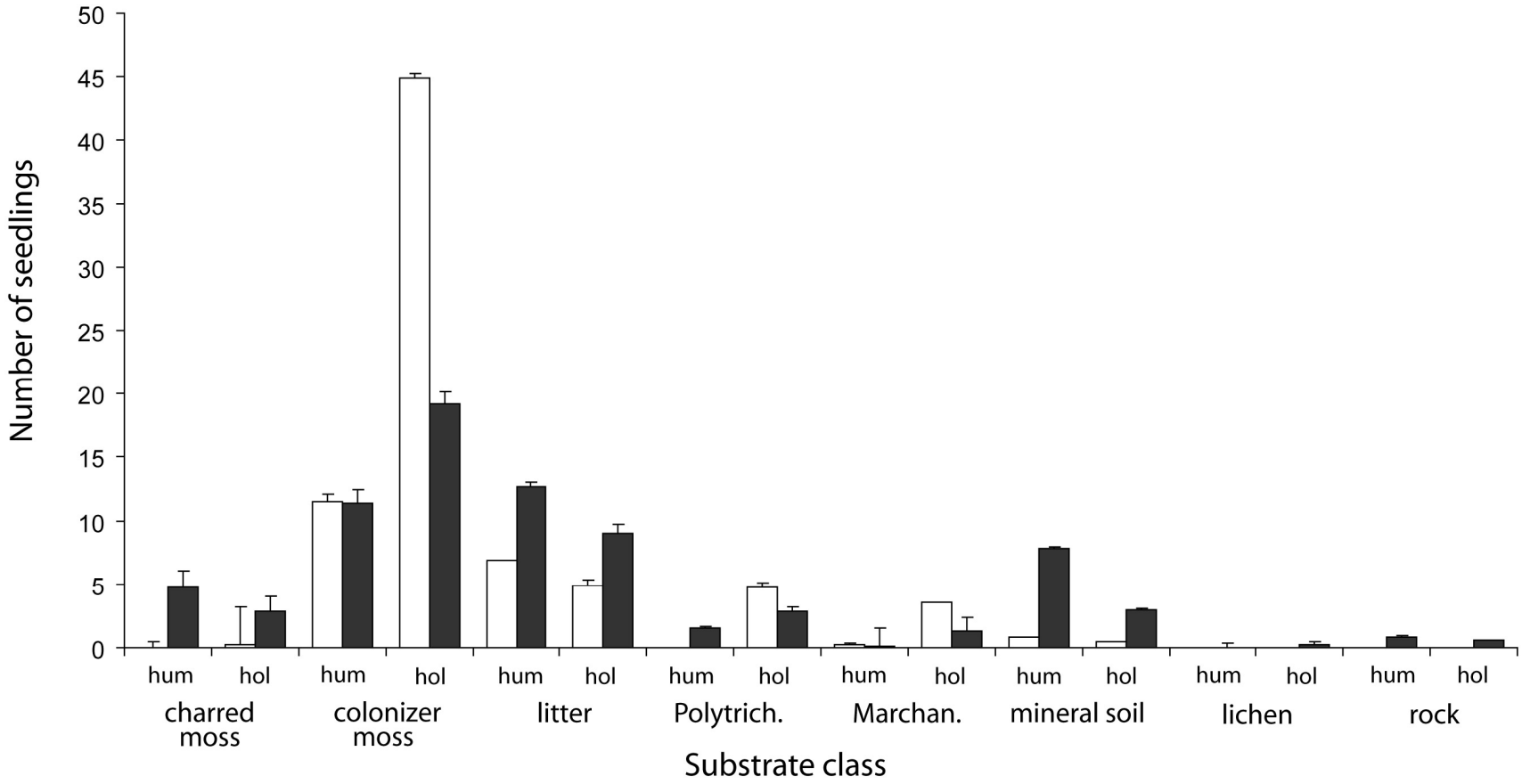

Figure 4-5: Observed (white) and expected (black) number of black spruce seedlings found in short-interval burned stands (mean ± SE; n=8), categorized by substrate class (Polytrich.=*Polytrichum* sp.; Marchan.=*Marchantia* sp.) and microtopography (hum=earth hummock; hol=hollow).

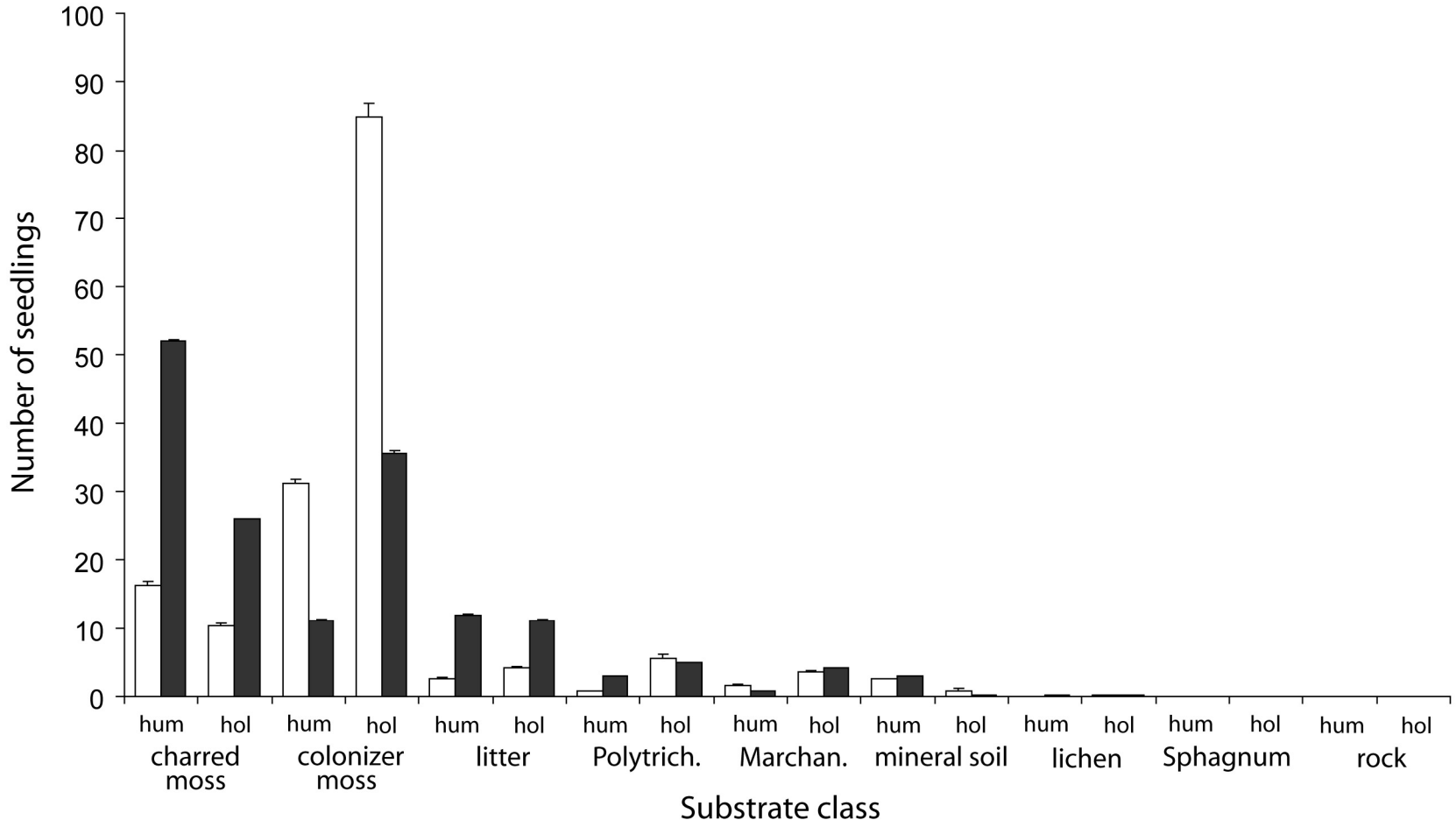

Figure 4-6: Observed (white) and expected (grey) number of black spruce seedlings found in long-interval burned stands (mean ± SE; n=8), categorized by substrate class (Polytrich.=*Polytrichum* sp.; Marchan.=*Marchantia* sp.) and microtopography (hum=earth hummock; hol=hollow).

species (black spruce: χ^2=337, p<0.0001; white spruce: χ^2=125, p<0.0001; Alaskan birch: χ^2=107, p<0.0001). In MF stands, what little seedling emergence occurred did so primarily on Sphagnum moss substrate, which had higher than expected seedling counts (black spruce: χ^2=466, p<0.0001; white spruce: χ^2=42, p=0.0002).

Soil moisture was positively correlated with colonizer moss cover in burned sites (t=4.30, df=30, p<0.001). The number of black spruce emergents was positively correlated with the colonizer moss cover in burned sites (t=2.55, df=30, p=0.008), whereas Alaskan birch and white spruce were not.

4.3.3 Environmental characteristics

SOH thickness, calculated as site means, differed significantly from MF to LI to SI burns (F=26.87, p<0.001, df=2; Figure 4-7a). Microtopography had no effect on SOH thickness (F=0.91, p=0.34, df=1) and I did not detect a significant interaction between the effects of fire history and microtopography on SOH thickness (F=0.07, p=0.93, df=2).

Soil temperature differed significantly from MF to LI to SI stands (F=55.98, p<0.001, df=2; Figure 4-7b). Microtopography had a significant effect on soil temperature where hummocks had warmer soils than hollows (F=15.89, p<0.001, df=1). I did not detect a significant interaction between fire history and microtopography (F=0.58, p=0.56, df=2).

Fire history and microtopography interacted to have a significant effect on soil moisture, where hummocks in MF stands were drier than hollows in LI stands (t=-2.28, p=0.03, df=2). Soil moisture differed significantly between fire history classes (F=19.64, p<0.001, df=2) and microtopography (F=23.85, p<0.001, df=1). Soil moisture was greatest in MF stands, and decreased in LI and SI stands, respectively (Figure 4-7c). Within each fire history class, hollows were wetter than earth hummocks.

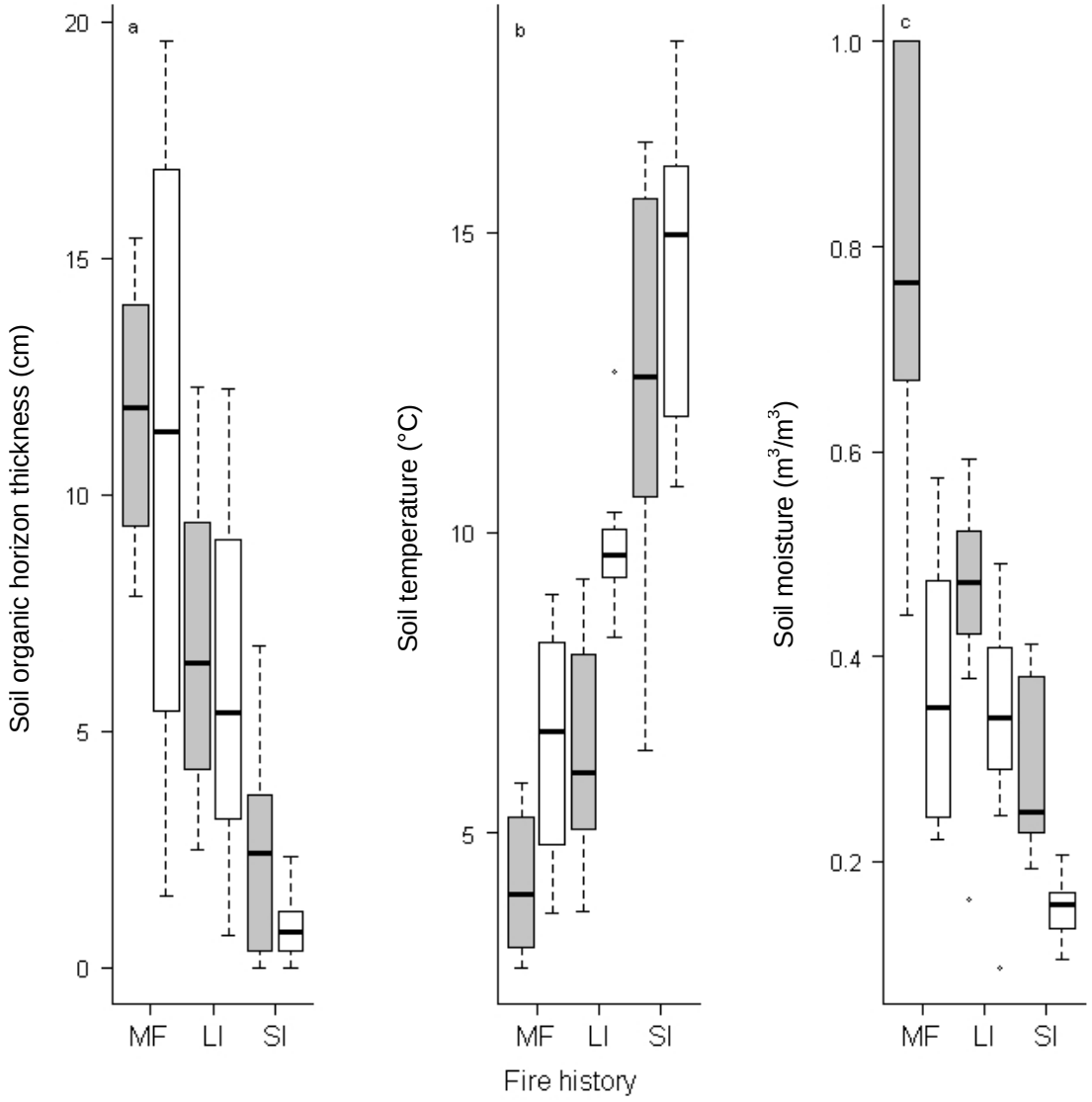

Figure 4-7: Summary of (a) soil organic horizon thickness, (b) soil temperature (^{o}C), and (c) soil moisture (m^3 water/m^3 soil) grouped by fire history and microtopography Fire history classes are: MF=mature forest, LI=long-interval burned, and SI=short-interval burned (n=8 sites/fire history class). Box colour indicates microtopography: plots were located on earth hummocks (white) and in hollows (grey). Soil temperature and soil moisture were measured once in each sampling plot (n=3 plots/microtopography within each site) in July 2009.

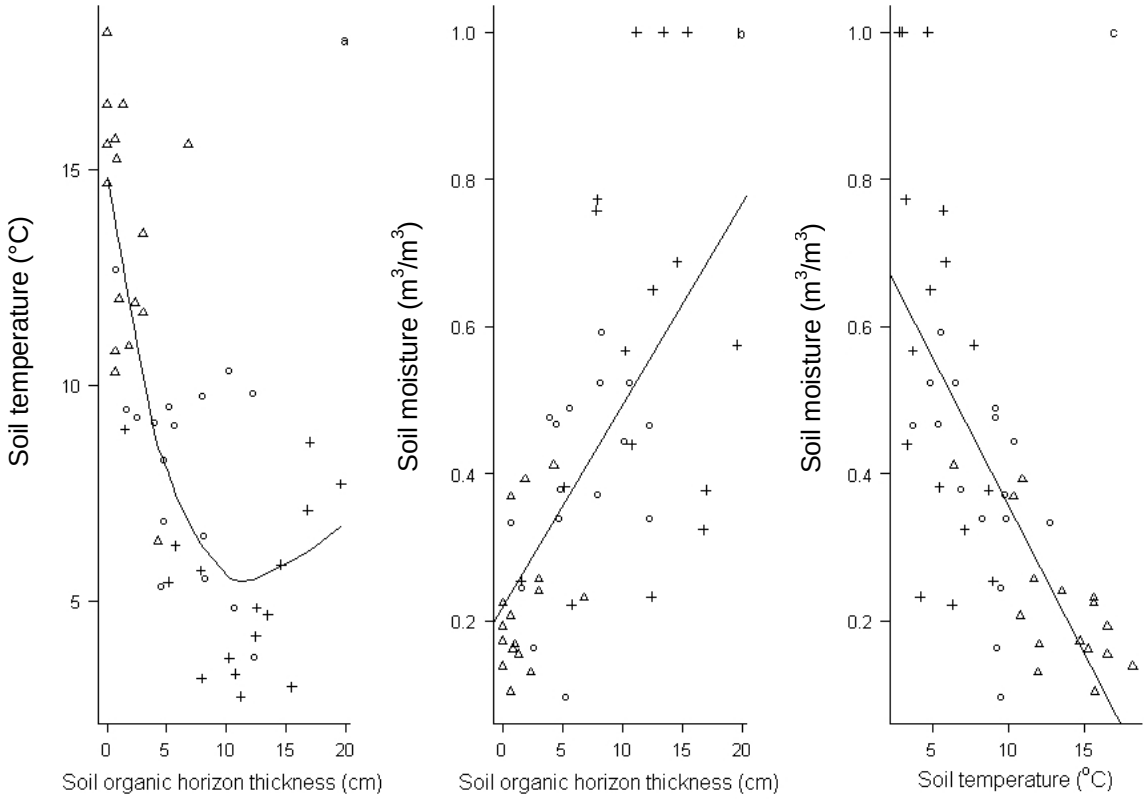

Figure 4-8: Relationship between soil organic horizon thickness (cm) and (a) soil temperature or (b) soil moisture, and (c) soil temperature and soil moisture in the 24 experimental sites (n=8/fire history class). Measurements were taken in mature forest (plus signs), long-interval burned (circles), and short-interval burned (triangles) stands. Each point represents the mean of six measurements taken in each experimental site. Soil temperature and soil moisture were measured once in each sampling plot (n=6 plots/site) in July 2009.

In addition to being individually affected by fire history, the environmental variables soil moisture, soil temperature, and SOH thickness were closely related (Figure 4-8). SOH was negatively correlated with soil temperature ($t=-6.14$, $df=46$, $p<0.001$; Figure 4-8a) and positively correlated with soil moisture ($t=5.53$, $df=46$, $p<0.001$; Figure 4-8b). Soil temperature and soil moisture were thus negatively correlated ($t=-7.11$, $df=46$, $p<0.001$; Figure 4-8c).

Depth of thaw did not differ between LI and SI stands ($F=1.3$, $df=1$, $p=0.21$, although both LI and SI had deeper thaw than MF stands ($F=58.0$, $df=1$, $p<0.001$, and $F=20.0$, $df=1$, $p=0.001$, respectively). As discussed in Chapter 3, the depth of thaw in LI and SI stands was often deeper than the length of the probe (26 and 29% of measurements, respectively), thus I may not have captured the actual depth of thaw in these stands.

4.4 DISCUSSION

4.4.1 Fire history and species effects

Fire history exerts a major control on species establishment and growth in the northern boreal forest stands studied here. For example, planted seedlings of all species had the greatest growth in SI stands, likely due to warmer soils and presumably more available nutrients. In contrast, MF stands, which had cold, wet soils, had the poorest growth of all species. A number of species-specific patterns were also identified. Seedling emergence, standardized by mass of seed planted, showed that black spruce emergence was greatest, followed by Alaskan birch. White spruce planted seedlings had the greatest growth performance of all species. Trembling aspen seedling growth was the poorest of all species tested. How can these results be reconciled in order to further our understanding of seedbed limitations on boreal forest succession? Below, I discuss in detail the interactions of fire history, seedbed condition, and species-specific adaptations that I hypothesize are driving these observed patterns.

4.4.1.1 Conifers

Black spruce seedling emergence was greatest in hollows in LI stands, where soil moisture was greatest. Seedlings also emerged on earth hummocks of LI and SI burned stands, and in SI hollows, but to a lesser extent. More Eagle black spruce were winter-killed than other species, which was likely due to their poor condition at the time of planting rather than the experimental treatment. Planted black spruce seedlings from both populations died more due to local environmental conditions, specifically desiccation, than by other causes. All of these metrics indicate that black spruce performs best in moist soils. Black spruce have adapted to succeeding in this type of environment, which explains their dominance as a northern treeline species (Black & Bliss, 1980). White spruce seedling growth and emergence was markedly better in SI stands than black spruce seedlings. White spruce prefers warmer, drier soils than black spruce, which can tolerate cold, wet soils (Burns & Honkala, 1990). There was also a contrast in seedling survival, due in part to seedling condition at the time of planting, but also due to white spruce's preference and tolerance of warmer and drier soils.

4.4.1.2 Deciduous species

Relative to MF stands, Alaskan birch seedlings emerged well in LI and SI stands, and the plots with the most birch seedlings occurred in SI burned hollows. Planted birch seedlings grew very well in SI stands, significantly better than LI stands. Alaskan birch is generally an upland species, and thus excelled on the warmer and drier microhabitats available in SI stands, similar to the patterns observed for white spruce.

Birch and aspen seedling death was most often caused by animals, predominantly herbivory. It is not surprising that more deciduous species were killed by herbivory than conifers, as they are more palatable to herbivores (McInnis *et al.*, 1992). It does suggest, however, that herbivory may limit the recruitment of deciduous species after fire, depending on the density of

local herbivores, such as snowshoe hares. This is supported by the increased survival of deciduous species planted in mature forest stands, where herbivore density was presumably lower than post-fire stands due to reduced browse availability. Conifer survival was not influenced by fire history; thus the mechanism influencing seedling survival between fire history classes is a deciduous-specific effect.

The most distinguishing response of our experiments on *Populus* spp. was that no balsam poplar seedlings emerged from seed, despite the seed's viability. Balsam poplar and trembling aspen seedlings are extremely sensitive to desiccation once they have emerged from the seed coat. They require consistent moisture availability for several weeks after emergence in order to become established, in part due to their small seed size that contains little carbohydrate stores for early survival (Burns & Honkala, 1990). When planted at the established seedling stage, trembling aspen performed well in SI stands. As with Alaskan birch, a portion of the trembling aspen I planted were killed by herbivory. The increased survival of trembling aspen on earth hummocks may have been due to an intolerance to periods of standing water in hollows (Burns & Honkala, 1990), for example during the spring melt. Trembling aspen is also affected by cold soils, which reduce root growth (Landhausser *et al.*, 2001).

Trembling aspen more commonly reproduces clonally than by seed (Zasada *et al.*, 1992). As there is no local stand of trembling aspen in the study area, it was important to test whether *Populus* spp. could recruit from seed that could potentially be wind dispersed into the study area from a stand in the region. Several studies have demonstrated aspen reproduction from seed (e.g., Zasada *et al.*, 1983; Johnstone & Chapin, 2006a), and trembling aspen regeneration has occurred after high severity fire in southern Yukon, despite the absence of local individuals to initiate clonal reproduction (Johnstone & Chapin, 2006b). Although I did not observe any balsam poplar

emergence from seed, planted trembling aspen did well in the warm, dry microhabitats present in SI stands. If individuals were present for clonal regeneration after fire, it is likely that aspen could become well established in a stand following a SI fire, particularly given similar findings in southwestern and central Yukon (Johnstone & Chapin, 2006b).

4.4.2 Seedbed effects

Regardless of species, seedling emergence in SI stands primarily occurred on colonizer moss substrate, where a thin cover of *Ceratadon*-type moss had established in the years since the 2005 fire. The areas where moss beds occurred at the time of my survey were those where moss was able to colonize and survive, and thus are indicative of relatively consistent moisture conditions. I hypothesize that the dense colonizer moss beds were able to retain moisture longer than other substrates, such as mineral soil, that occurred in SI burns. Thus, the colonizer moss beds created a microhabitat where seedlings could emerge under relatively stable moisture conditions, a critical requirement for germination of the species tested here (Greene *et al.*, 1999). In contrast to colonizer moss, seedling emergence was consistently less than expected on charred moss substrates. Colonizer moss substrates were charred moss patches immediately after fire, until colonized by *Ceratadon*-type moss. It is possible that the areas that persisted as charred moss were those that were inhospitable to moss colonization, perhaps due to inadequate soil moisture.

The effects of soil moisture and fire history interactions, and soil moisture and microtopography interactions on Alaskan birch emergence supports my hypothesis that soil moisture limits recruitment in SI stands. Microhabitats that were shown to be dry, i.e., SI stands and hummocks, had large increases in birch emergence when soil moisture was high. I did not detect a main effect of soil moisture on seedling emergence in any of my models. However, my

observed emergence patterns mimicked soil moisture patterns in LI and SI stands. I detected a difference in soil moisture between fire history classes and microtopography, suggesting that the soil moisture effect may have been masked by the effect of microtopography on the seedling emergence. This is further supported by the positive relationship I detected between colonizer moss cover and soil moisture in burned stands. I have already shown that fire history acts as the major control of recruitment in these northern boreal stands. Moisture variability within burned stands may be acting as a secondary control on seedling recruitment.

Seedling emergence was consistently higher in hollows than on earth hummocks in SI and LI stands, regardless of species seeded. Here and elsewhere, it has been documented that hollows are wetter and colder than earth hummocks (Black & Bliss, 1980; Kokelj *et al.*, 2007), which may explain the success of black spruce in these microhabitats. What was surprising was that more white spruce and birch also emerged in hollows than on earth hummocks. This is counterintuitive, as it is well documented that white spruce and birch excel on well-drained, warm soils (e.g., Zasada *et al.*, 1992; Delong *et al.*, 1997). To understand this contradiction, I looked at the location of the hollows where these species thrived: SI stands. Earth hummocks in SI stands were the driest of all microhabitats we measured and were likely too dry for seedlings to survive. Seedlings that emerged during periods of high precipitation (e.g., 2008) may have died due to desiccation during subsequent dry periods. This moisture limitation is further corroborated by the emergence of black spruce on hummocks in LI burns, but not SI burns. LI burned hummocks had higher moisture, approximately equivalent to SI hollows, where black spruce seedlings were able to emerge well. Post-fire reductions in recruitment due to low water availability on earth hummocks have also been documented in black spruce stands in Northwest Territories (Black & Bliss, 1980).

Seedling emergence was nearly nonexistent for all species seeded in MF stands, confirming my previous conclusion that substrate limits black spruce recruitment in mature forests (Chapter 3). The few seedlings that did emerge occurred almost entirely on Sphagnum moss. As with emergence in more recently burned stands, this is likely due to moisture availability, although caused by different factors. The substrate of mature forest stands was dominated by mosses and lichens (Brown and Johnstone, unpublished data). Moss and lichen substrates are prone to large fluctuations in temperature and moisture due to their porous nature (Charron & Greene, 2002; Johnstone & Chapin, 2006a). If a seed is able to germinate on this type of surface, seedlings are likely to die due to desiccation (Charron & Greene, 2002; Jayen *et al.*, 2006). In contrast, I hypothesize that the colonizer moss substrate was less porous and able to retain more water (C.D. Brown, personal observation).

4.4.3 Constraints on post-fire regeneration

The results of this research lead to the hypothesis that seedling emergence is more of a limiting step to post-fire recruitment than seedling growth and survival. Once a seedling becomes established, which I mimicked using planted seedlings, it tended to survive and grow well in burned areas. The microhabitat conditions in which seedlings grew in SI stands contributed to increased biomass and growth. The warmer, drier soils of SI stands may have provided more available nutrients to seedlings than LI stands (Epstein *et al.*, 2000), although if SI stands become too dry, the effects of moisture stress would likely outweigh that of available nutrients. These dry conditions are most likely the result of a combination of factors. During the second fire, the depth of thaw may have increased beyond that of LI stands, increasing soil drainage. The second fire also reduced SOH thickness beyond that which typically occurs following a LI fire (Chapter 5). Since SOHs hold much of the soil moisture available to young seedlings,

thinner SOH result in drier microhabitats. The absence of trees and shrubs in SI stands may reduce the likelihood that snow will become trapped on the landscape, and open areas often have increased rates of spring melt than forested stands (Winkler *et al.*, 2005). This may mean that less snow is available to melt in SI stands than LI or MF, further reducing soil moisture, or that melting occurs more rapidly thus increasing runoff.

Mature forests do not provide suitable habitat for seedling emergence or planted seedling growth. Seedling emergence of all species was nearly absent in MF stands. Planted seedlings survived, but grew little, likely due to cold soils limiting nutrient availability. The patterns I have documented contribute further evidence to the case that fire is required for community change in the boreal forest. The partial combustion of the forest floor reduces competition and creates a flush of available nutrients after fire (Johnson, 1992; Payette, 1992). Warmer soil temperatures are caused by the deepening of the permafrost table and increased absorption of solar radiation by the charred forest floor (McGuire *et al.*, 2006; Schuur *et al.*, 2008). In combination, these conditions create favourable microhabitats for seed germination, seedling emergence, establishment, and growth. Species must establish during this short window of opportunity after fire, before seedbed composition becomes unsuitable for recruitment, as seen in my MF stands. The short opportunity observed for seedling establishment in my study area provides further evidence for using recruitment patterns immediately after fire to predict future patterns in forest composition.

4.4.4 Conclusions

Using field experimentation, I have identified links between species recruitment, seedbed condition, and fire history in northern boreal forest stands. I have already shown that seed availability constrains black spruce stand self replacement after SI fire (Chapter 3). My aim here

was to identify links between specific substrates and seedling emergence in the absence of seed limitation and to compare the performance of potential canopy dominants. Growth of all tree species tested was greatest in SI stands, indicating that these stands have favourable habitat for forest regeneration. Given the seed limitation of black spruce in SI stands, the seedbed is open for colonization by any of the regional tree species that can disperse to the site, as black spruce no longer has an advantage. Microhabitat conditions did effect species establishment and growth, but were less important than the effects of fire history. However, fire and microtopography effects on microhabitat suggest that moisture and temperature interact to determine the optimal habitat. The optimal habitat detected in the study area was found to be open for colonization and warm, but not too dry. The results lead me to predict a positive effect of warming, in the form of direct climate effects or indirect fire effects, on post-fire recruitment potential. However, this pattern could reverse, becoming a negative effect, if conditions become too dry. The results presented here suggest that early moss growth may be an excellent indicator of seedbed quality in northern boreal forest stands.

5.0 HOW DOES INCREASED FIRE FREQUENCY AFFECT CARBON LOSS FROM FIRE? A CASE STUDY IN THE NORTHERN BOREAL FOREST

FOREWORD

In Chapters 2, 3, and 4, I have presented data on the structure and composition of northern boreal forest stands that have undergone long- and short-interval fires. In this final data chapter, I quantify the carbon storage capacity of these northern black spruce stands, and discuss the impacts of a shortened fire return interval within the context of the global carbon cycle. This chapter is modified from:

Brown, C.D. and Johnstone, J.F. How does increased fire frequency affect carbon loss from fire? A case study in the northern boreal forest. *In press*. International Journal of Wildland Fire

5.1 INTRODUCTION

The boreal forest plays a major role in the global carbon cycle as it contains more than one-third of the world's carbon stored in terrestrial ecosystems (Kasischke, 2000; McGuire *et al.*, 2002; Tarnocai *et al.*, 2009). Two-thirds of that carbon is stored in organic matter that has accumulated in forest soils and peat deposits, while the remainder is stored in above-ground vegetation biomass. Carbon storage is determined by net ecosystem production, or the balance between the amount of carbon a system fixes as biomass (gross primary production) and releases through ecosystem respiration (Chapin *et al.*, 2006). Net ecosystem production differs from the net ecosystem carbon balance (i.e., the rate of carbon accumulation) because of carbon fluxes caused by fire or other factors.

Fire is the dominant disturbance affecting net ecosystem productivity in the boreal forest of North America (Bond-Lamberty *et al.*, 2004; Bond-Lamberty *et al.*, 2007; Jonsson & Wardle, 2010). During fire, organic matter is oxidized to inorganic carbon and released from the ecosystem (Chapin *et al.*, 2006). Forests become a source of carbon after fire as the rate of decomposition exceeds carbon fixation through primary productivity (Amiro *et al.*, 2003; Chapin *et al.*, 2006; Kashian *et al.*, 2006). As the stand regenerates and primary production increases, the boreal forest returns to acting as a carbon accumulator, sequestering carbon in soil, detritus, vegetation, and dead wood (Kasischke *et al.*, 1995; Harden *et al.*, 2000; Kashian *et al.*, 2006). The boreal forest has a historic role as a net accumulator of carbon (or a carbon 'sink') and is an important contribution to climate-ecosystem feedbacks. Thus, there is currently a great interest in how a change in climate will affect the structure and function of this ecosystem. Recent literature has called for the 'urgent' preservation of the boreal forest (Bradshaw *et al.*, 2009), in part because of its important role in terrestrial carbon storage (Kasischke, 2000).

Fire frequency varies widely across different regions of the boreal forest, but in the boreal forests of North America fire return intervals are generally long enough for trees to re-establish and recover to mature stands before the stand burns again (Heinselman, 1981; Payette, 1992). In the western boreal forest of North America, fires occur in a given area approximately every 100 years (Johnson, 1992). However, fire frequency is predicted to increase as the climate warms (Flannigan *et al.*, 2005; Soja *et al.*, 2007; Balshi *et al.*, 2009), and increased fire activity is already being noted in some parts of the boreal forest (Gillett *et al.*, 2004; Kasischke & Turetsky, 2006). Changes in the fire regime will strongly affect the structure and function of boreal ecosystems (Weber & Flannigan, 1997), with important implications for the global carbon cycle due to altered patterns of carbon accumulation and storage (Kasischke *et al.*, 1995; Grace *et al.*, 2002; Bond-Lamberty *et al.*, 2004).

The main objective of this research was to quantify and compare the amount of carbon stored and consumed by fire in northern boreal forests that have burned with a long versus short fire interval. Natural variations in recent fire frequency provided an opportunity for a case study assessing the effects of a shortened fire return interval on net ecosystem production in northern black spruce forests. Typically, carbon lost during fire in the boreal forest is regained once the stand has recovered to maturity (Kashian *et al.*, 2006). However, this equilibrium may be interrupted by a change in the disturbance regime (Kasischke *et al.*, 1995; Lecomte *et al.*, 2006). I hypothesized that a shortened fire return interval would result in greater consumption of carbon from black spruce (*Picea mariana* [Mill.] BSP) forest stands than those that have experienced a typical fire return interval (i.e., 80-150 years). More specifically, short-interval burned stands will have less above- and below-ground organic matter post-fire than long-interval burned stands. A shortened interval between fires means that stands will not have recovered to pre-fire

carbon levels prior to the most recent fire. Thus, a portion of the carbon that was not consumed during the initial fire will be consumed during the second. This incremental loss of carbon due to repeated disturbance may lead to a long-term decline in net ecosystem production (even when forests may continue to function as a carbon sink after a fire) due to the shift in stand age before fire, and subsequent reduction of long-term carbon stores.

5.2 METHODS

5.2.1 Study area

Study sites were established in conifer-dominated forests of the Eagle Plains Ecoregion in the Taiga Cordillera Ecozone (Smith *et al.*, 2004) of northern Yukon (66°06'56"N, 137°16'11"W). Eagle Plains is part of Beringia, which remained unglaciated during the Wisconsonian period, and the terrain is composed of rolling hills with fine grained loess soils over weathered bedrock. Eagle Plains has a continental climate. The nearest weather stations, in Dawson City (~290 km SW; 64°02'35"N, 139°07'40"W) and Old Crow (~190 km NW; 67°34'14"N, 139°50'21"W) YT, have mean annual air temperatures of -4.4°C and -9°C, and monthly mean temperatures of -26.7°C and -31.1°C in January, and 15.6°C and 14.6°C in July (Environment Canada, 2011). The mean annual precipitation is 324 mm in Dawson City and 266 in Old Crow, about half of which falls as rain in the summer in both locations (Environment Canada, 2011). Underlain with continuous permafrost, the active layer of seasonally thawed ground extends less than 1 m below the soil surface (20 cm under hollows, 90 cm under hummocks; Tarnocai *et al.*, 1993) and has mean annual ground temperatures near the soil surface of -3°C (Johnston, 1980). The surface terrain is dominated by small-scale microtopography in the form of earth hummocks caused by differential freezing and thawing of soil. The soil thermal

regime is disrupted by fire, which deepens the active layer and releases water from the frozen soil (Schuur *et al.*, 2008).

Ninety percent of the region is composed of sub-arctic coniferous forest, most of which is dominated by black spruce (Smith *et al.*, 2004). Black spruce has a high tolerance for cold, wet soils, giving it a competitive advantage in northern forests (Black & Bliss, 1980). Black spruce is adapted to recovery after fire, having semi-serotinous cones that maintain an aerial seed bank for several years and open to release seeds after fire (Johnson, 1992).

Study sites were selected from the mosaic of burned and unburned black spruce forest found in the Eagle Plains region (Figure 5-1). Two fires burned in this area in the early 1990s (1990: 33,500 ha and 1991: 4,800 ha), followed by a 69,000 hectare fire in 2005 that partially overlapped both the 1990 and 1991 burns. As summarized in Chapter 3, Fire Weather Index and Fire Behaviour Prediction values (Wagner, 1987; Lee, 1995) calculated for the study area for a two week period surrounding the date of ignition of each fire suggested that the 2005 fire burned in more volatile conditions than the 1990 and 1991 fires (Table 5-1; R. Carr and P. Englefield, unpublished data). The period of the 2005 fire had several individual days of higher Fire Weather Index values than the 1990 and 1991 fire periods, which is reflected in the sizes of each fire. Despite the difference in estimated conditions during the time of ignition, all three fires were of low-moderate severity in long-interval burned stands, as indicated by the presence of fine branches on fire-killed trees.

The fire history mosaic at Eagle Plains allowed me to sample unburned, long-interval burned, and short-interval burned sites immediately adjacent to one another (Figure 5-1; Table 5-2). Sites in three stages of post-fire forest recovery were selected for study: 1) mature unburned forest (previous fire ~77 years ago; MF), 2) early successional stands following a long-interval

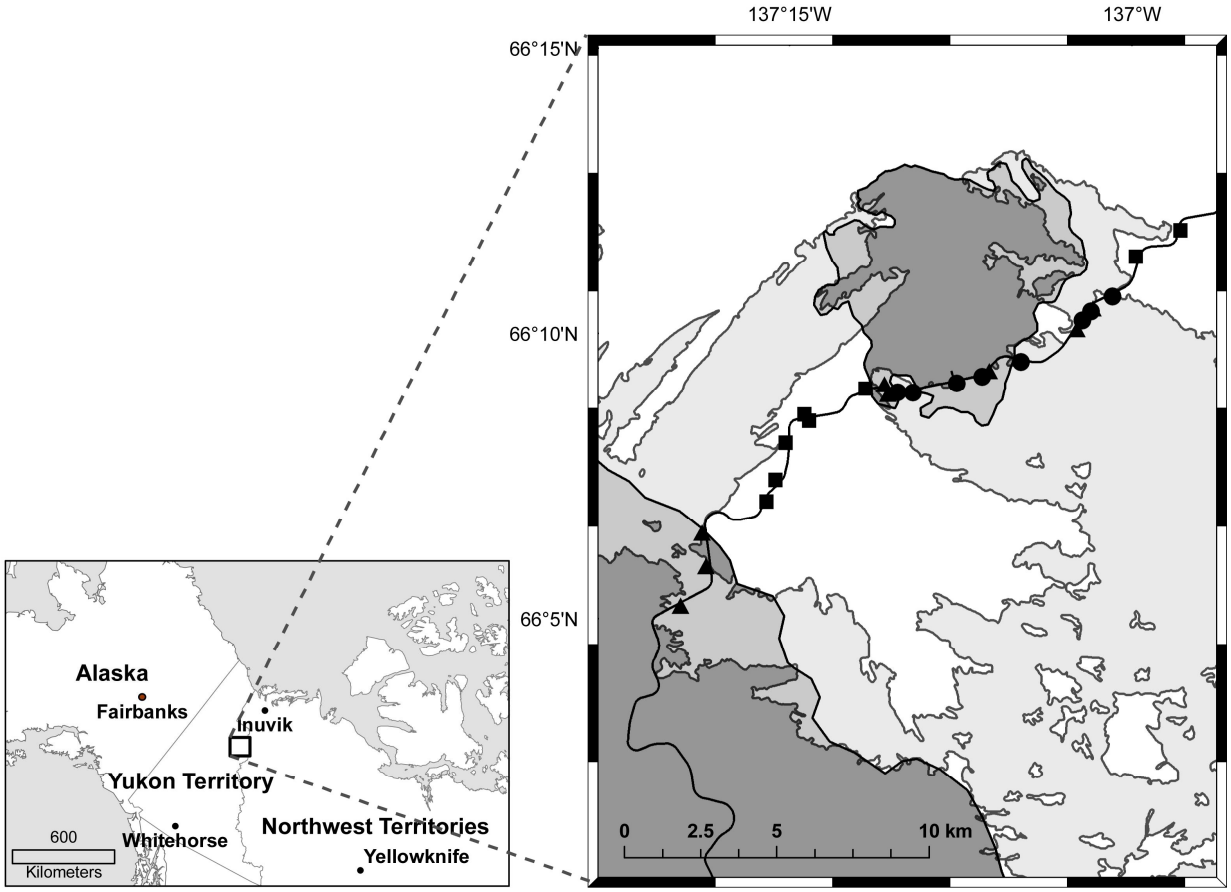

Figure 5-1: Study area in northern Yukon, Canada, with areas burned in 1990/1991 (dark grey) and 2005 (light grey) indicated, and the 1990s and 2005 fire overlap (medium grey). Study sites (n=8/fire history) were established in mature forest (squares), long-interval burns (circles), and short-interval burns (triangles).

Table O: Range of fire weather index and fire behaviour prediction component values for the study fires in the two weeks surrounding the date of ignition (R. Carr and P. Englefield, unpublished data).

Year of fire	Area burned (ha)	Fine fuel moisture code	Duff moisture code	Drought code	Initial spread index	Build up index	Fire weather index	Rate of spread (m min^{-1})	Surface fuel consumption (kg m^{-2})	Total fuel consumption (kg m^{-2})
1990	33500	54.7-89.2	13.7-33.3	327-398	0.3-7.3	25-55	0-16	0.02-2.7	0.8-1.2	0.8-1.4
1991	4800	52.1-84.2	20.2-29.7	277-360	0.3-3.0	34-49	0-9	0.03-0.9	1.0-1.3	1.0-1.2
2005	69000	49.4-88.2	19.6-40.5	328-384	0.4-8.2	35-64	1-21	0.09-10.1	1.7-2.6	1.8-3.2

burn (fire in 2005 following ~94 years fire-free; LI_{2005}), and 3) early successional stands following a short-interval burn (fire in both 1990/91 and 2005; SI). Long-interval burned sites that were last burned in 1990 and 1991 were also sampled; both for comparison to the LI_{2005} sites and to estimate the condition of the SI burned sites prior to the 2005 fire.

I placed eight 2 m x 30 m belt transects in upland stands within MF, LI_{2005}, and SI burned stands (for a total of 24 transects). Six transects were placed in LI stands burned in 1990 and 1991. In all cases, transects were selectively placed in an attempt to capture the natural variation of stand characteristics in each burn (e.g., soil moisture, slope, and microtopography; Table 5-2). All study sites were accessed from the Dempster Highway, a gravel road that provides the only road access to the study area, and were positioned a minimum of 80 m from the road to avoid road effects on environmental conditions (Auerbach *et al.*, 1997). All belt transects had an east-west orientation. Samples were stratified by hummock-hollow microtopography, as hummocks typically have drier, warmer soil conditions than the hollows found between hummocks.

5.2.2 Soil and stand measurements

I sampled SOH thickness and bulk density in July 2008. A 10 cm x 10 cm sample of the SOH, from forest floor to mineral soil surface, was excavated from three hummocks and three hollows randomly selected along the sampling transect in each study site, for a total of six samples per site. The thickness of each organic horizon was measured, and then averaged to obtain a single mean value for each site. Surface bulk density, calculated using the top five cm of each SOH sample, was measured for a comparison of stand characteristics across sites. Depth of thaw (cm) was measured with a probe in five hummocks and five hollows along the same transect in August 2008. When depth of thaw exceeded the length of the probe, depth was recorded as >1.2 m (probe length).

In MF and LI stands, I measured diameter at breast height (DBH) of all pre-fire trees (live or dead, standing or fallen) that were originally rooted within the 2 m x 30 m belt transect and used these data to calculate stand density, basal area, and canopy biomass. As no trees were present in SI stands, no stem measurements were made. Field observations in the LI and SI stands indicated that all trees were killed in the fires, as no survivors were found. Thus, live trees were measured in MF stands and fire-killed trees were measured in burned stands. Biomass resulting from post-fire regeneration was not measured in LI or SI stands.

5.2.3 Estimation of carbon consumption and stores

I used equations developed for black spruce forests in interior Alaska to calculate carbon consumption and storage from field measurements in our study area. I estimated the thickness of SOH consumed during fire as the distance between the surface of the burned SOH and the uppermost adventitious roots on a pre-fire black spruce stem (termed adventitious root height [ARH]; Kasischke & Johnstone, 2005; Boby *et al.*, 2010; Figure 5-2). This method takes advantage of adventitious roots that form on the stems of black spruce trees as the forest floor thickens and the soil around deeper roots becomes increasingly cold and wet (LeBarron, 1945). Previous research in similar forest types in Alaska has shown that the position of the uppermost adventitious roots on a black spruce tree is a good indicator of the height of the green moss layer at the top of the organic horizon (Kasischke & Johnstone, 2005; Boby *et al.*, 2010). As there is a time lag between moss growth and adventitious root initiation, I used the offset between the mean ARH in MF stands and surface of the organic horizon to estimate the correction factor between the uppermost adventitious root and the top of the moss layer (termed ARH offset; Boby *et al.*, 2010). In LI and MF stands, ARH measurements were made on the two closest individuals at 5 m intervals along a transect, starting at 0 m (14 individuals/site). I also applied

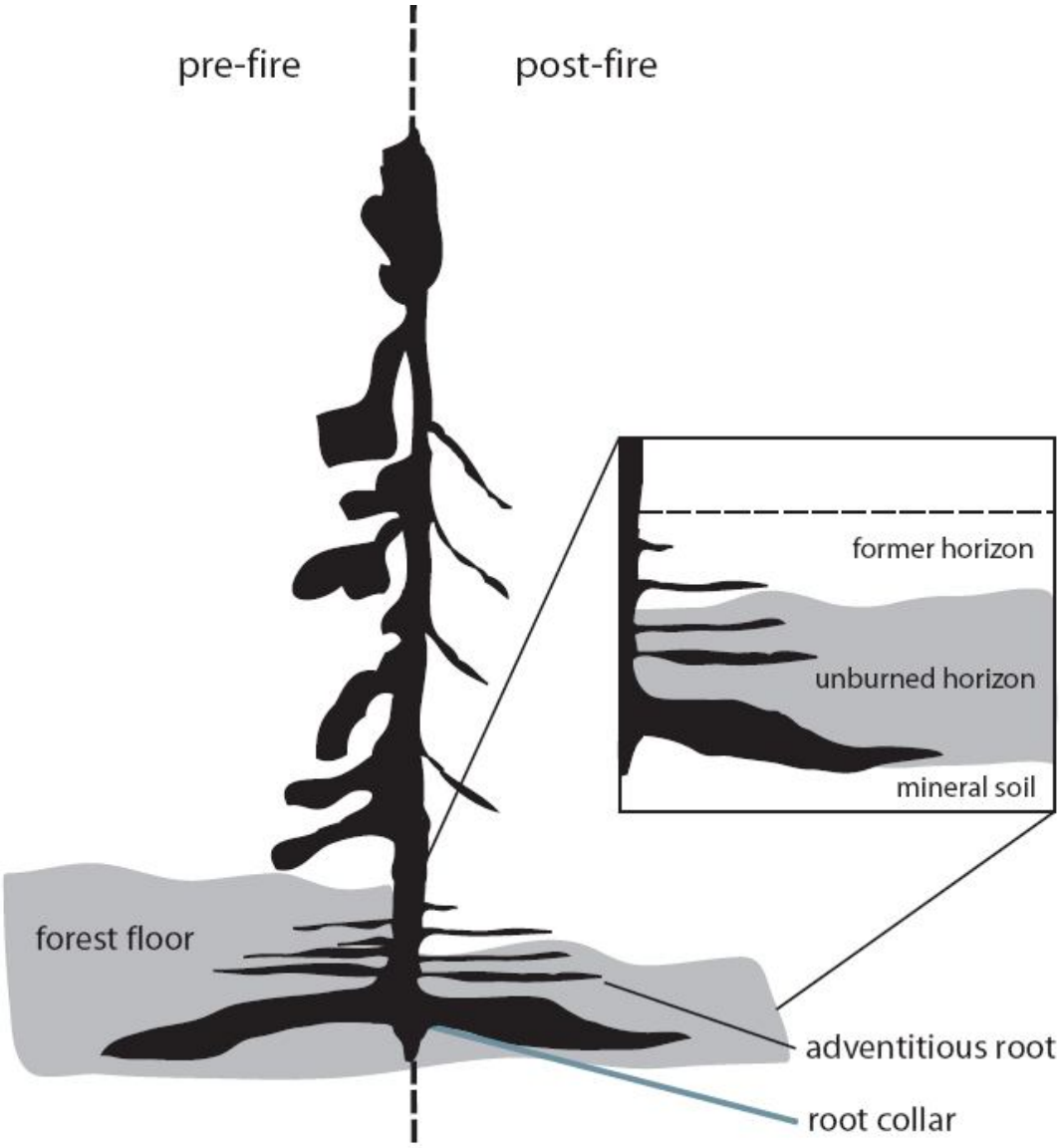

Figure 5-2: Diagram of a typical black spruce, illustrating soil organic horizon thickness and adventitious root exposure before and after fire.

the correction factor calculated by Boby *et al.* (2010) to account for the greater consumption of the organic horizon at the bases of trees than in random points in burned stands. Thus, the pre-fire soil organic horizon thickness (SOH_{pre}; cm) in LI stands was calculated following Boby *et al.* (2010):

$$SOH_{pre} = SOH_{post} + ARH + ARH_o + SOH_c$$

where SOH_{post} represents the post-fire SOH thickness (cm), ARH represents the adventitious root height (cm), ARH_o represents the adventitious root height offset (cm), and SOH_c represents the tree base correction factor (cm).

Carbon stored in the SOH was estimated using an empirical relationship between organic horizon thickness (cm) and soil organic carbon (SOC; kg m^{-2}) developed by Kane *et al.* (2007) from published data for similar black spruce stands in interior Alaska (r^2=0.64, $p<0.001$, n=23, β_0=2.39±0.50, β_1=0.16±0.03). I substituted post-fire (residual) organic horizon thickness for the thickness consumed used by Kane *et al.* (2007) in order to calculate carbon storage after fire.

I estimated black spruce canopy consumption by calculating the biomass of standing wood in LI and MF stands using published allometric equations for estimating whole-tree biomass of black spruce in interior Alaska (Yarie *et al.*, 2007; r^2=0.905, $p<0.05$, n=78, β_1=358.35±240.81, β_2=158.167±26.75). In the black spruce canopy, the carbon content of tree biomass was estimated as 53% of the canopy biomass, based on measurements by Susott *et al.* (1991) and following Kasischke *et al.* (2000).

The majority of black spruce biomass is made up of stem and coarse branches. Any needles or fine branches that were consumed during or shed after a fire would have a negligible

contribution to stand biomass. Thus, biomass estimates of LI_{2005} stands should be similar to MF sites. Since SI stands had no standing wood remaining in 2008, living or dead, I assumed that the biomass consumed was equal to the standing volume of pre-fire trees in LI_{2005} or live trees in MF stands.

5.2.4 Statistical analyses

Stand density, stand basal area, depth of thaw, and carbon content of wood were compared between MF, LI_{2005}, and SI stands using ANOVA. In recently burned sites, stand density and basal area represent the fire-killed trees still present in the stand. Total carbon stored was $\log_{10}$ transformed for the comparison between LI_{2005} and SI stands to better meet the ANOVA assumption of homogeneity of variance in the data. SOH thickness and carbon content were compared between unburned, LI_{2005}, and SI stands using a non-parametric Kruskal-Wallis (H) test, as the data did not demonstrate homogeneity of variance even after transformation. To determine if SI stands had similar characteristics to the LI_{2005} stands prior to the most recent fire, stand density, basal area, and adventitious root height were compared between $LI_{1990/91}$ and LI_{2005} stands using ANOVA. All statistical analyses were conducted using SPSS Statistics version 17.0 (SPSS Incorporated, Chicago, IL, U.S.A.).

5.3 RESULTS

The mean adventitious root height in LI_{2005} stands was 9.1 ± 0.3 cm (mean ± standard error, n=8 sites). The mean pre-fire thickness in the LI_{2005} stands was calculated as 17.7 ± 1.7 cm, based on post-fire organic horizon thickness of 6.4 ± 1.2 cm, a measured offset of 2.3 ± 0.4 cm between the uppermost adventitious root and the top of the organic horizon in MF stands, and a tree base correction of -0.4 cm in MF stands. Estimated means of pre-fire organic horizon thicknesses ranged from 12.1 – 24.8 cm across the eight LI_{2005} stands. This estimate of pre-fire

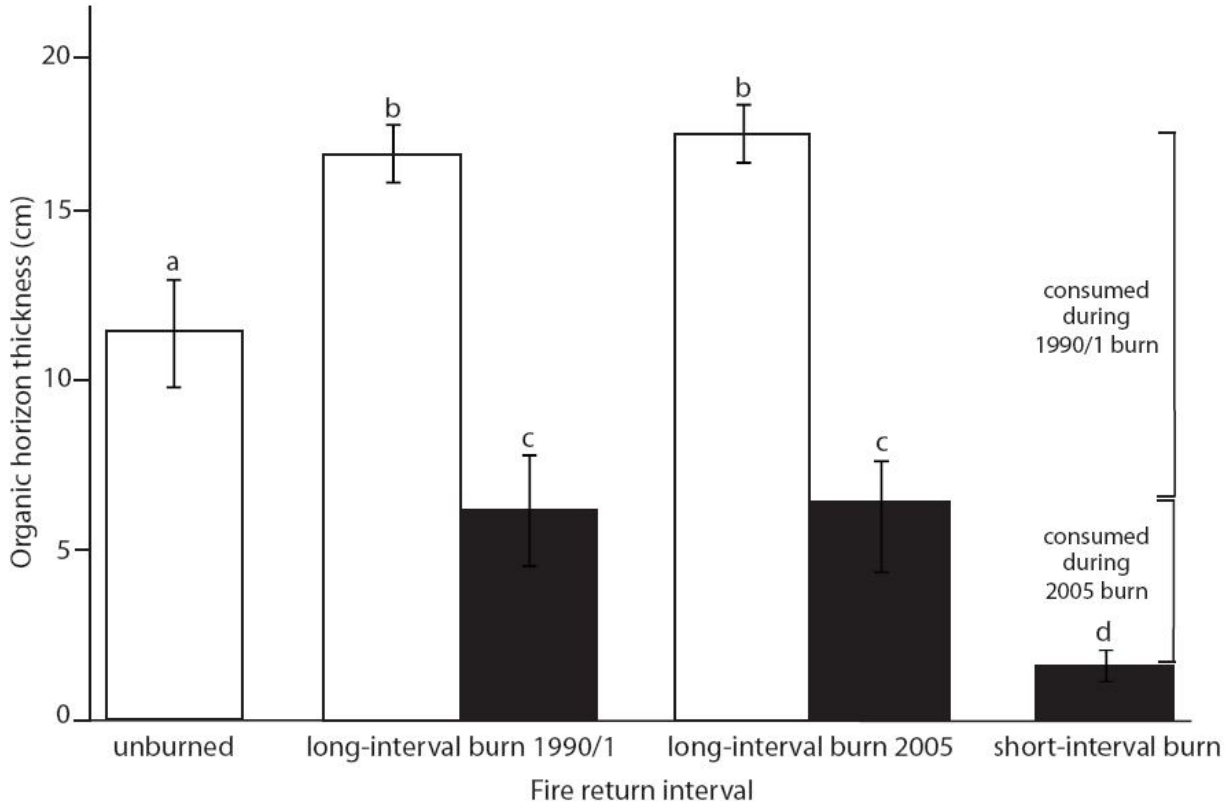

Figure 5-3: Soil organic horizon thickness (mean+/-1SE; cm) in mature forest (unburned), long-interval burned in 1990/1, long-interval burned in 2005, and short-interval burned treeline forest sites in northern Yukon. Unburned and pre-fire (calculated using adventitious root height) organic horizon thickness (white bars) are compared to post-fire thickness (black bars). The proportion of organic horizon consumed during the short-interval fires is indicated. Bars labelled with different letters were significantly different in a Tukey multiple comparison test following a significant single-factor analysis of variance.

organic horizon thickness was 6.3cm (55%) greater than observed thickness in MF stands ($F=7.7$, $df=1$, $p=0.01$; Figure 5-3). This result may accurately reflect pre-fire differences between the two forest classes, or the adventitious root method may have over-estimated pre-fire organic horizon thickness. However, the mean adventitious root height in LI_{2005} stands was not significantly different from the $LI_{1990/91}$ stands (9.2 ± 0.4 cm; $p=0.89$) and consequently there was no significant difference in my estimates of pre-fire organic horizon thickness at the LI_{2005} and $LI_{1990/91}$ stands ($F=95.3$, $df=1$, $p=0.99$, Figure 5-3). The similarity in pre-fire organic horizon thickness at the LI_{2005} and $LI_{1990/91}$ stands suggests that prior to the 2005 fire, SI stands contained an analogous amount of SOH biomass to LI_{2005} sites. MF stands were ~17 years younger than LI stands and may not yet have accumulated the organic matter present in the pre-fire LI stands.

The extant thickness of the SOH decreased between sites from MF to LI_{2005} to SI stands ($F=17.2$, $df=2$, $p<0.001$; Figure 5-3). Sixty-one percent of the SOH thickness was consumed during the long-interval fire, and 63% followed by 75% was cumulatively consumed over the two fire events that recurred after a short interval. In all stands, considerably more carbon was stored in the organic horizons than in wood biomass (Table 5-3). Stand density (trees/ha) did not differ between MF and LI_{2005} stands ($F=0.02$, $df=1$, $p=0.90$; Table 5-3) although stand basal area was marginally greater in the LI_{2005} stands ($F=3.9$, $df=1$, $p=0.068$; Table 5-3). The observed differences in tree basal area but not density between MF and LI_{2005} stands may be attributable to the younger age of MF stands (Table 5-2), and thus somewhat smaller tree sizes. In the SI stands, pre-fire tree stems, representing both the mature individuals burned in 1990/91 and new recruits established between 1990 and 2005, were completely consumed aside from the occasional, deeply charred stump or piece of wood. Stand basal area in $LI_{1990/91}$ stands, which presumably represent the pre-fire condition of the SI stands, was marginally less than MF stands ($F=3.9$,

Table P: General properties of stands sampled in this study. Range presented for slope and aspect, the remaining variables presented as mean ± 1SE. Aspect is separated into sites with eastern and western exposure. Stand age was calculated from ground-level stem sections.

Fire history class	Slope (%)	Aspect (degrees)	Stand age (years)	Depth of thaw (cm)	Proportion hummock	Surface bulk density (g cm^{-3})
Mature forest	3-11	eastern: 80-140 western: 309-331	77±3	40.3±2.2	59.4±2.3	0.29±0.06
Long-interval burn (2005)	0-6	eastern: 110-178 western: n/a	94±6	80.9±2.4	55.3±3.2	0.37±0.09
Short-interval burn	3-9	eastern: 75-166 western: 266-331	n/a	82.0±3.1	55.1±4.2	0.34±0.06

Table Q: Stand characteristics and carbon content in the study area in 2008 (mean±SE).

	Stand characteristics		Carbon content (g C m^{-2})		
Fire history class	Stand density[#] (trees ha^{-1})	Stand basal area[#] (m^2 ha^{-1})	Wood biomass	Organic horizons	Total
Mature forest	4583 ± 474	8.39 ± 1.03	834 ± 130	4209 ± 251	5044 ± 203
Long-interval burn (1990-91)	1488±128	5.29±1.18	507 ± 55	3433 ± 145	3940 ± 119
Long-interval burn (2005)	4729 ± 700	13.49 ± 1.89	970 ± 135	3418 ± 191	4388 ± 235
Short-interval burn	n/a	n/a	n/a	2654 ± 65	2654 ± 65

[#] Represents living trees in unburned stands and fire-killed trees in all remaining stands.

df=1, p=0.072) and significantly less than LI_{2005} stands (F=11.4, df=1, p=0.005). The $LI_{1990/91}$ stands were approximately the same age as LI_{2005} stands (91±2 and 94±6 years old, respectively), thus the observed difference in tree basal area may be due to site productivity.

Long interval fire did have an impact on ecosystem carbon stores, as post-fire carbon stores in LI_{2005} stands were marginally less than those in MF stands (F=4.5, df=1, p=0.053). Carbon stores in the SI stands were considerably less than in MF or LI stands (F=126.0, df=1, p<0.001, and F=50.4, df=1, p<0.001, respectively; Table 5-3). SI stands stored ~60% (2654 +/- 65 g C m^{-2}) of the post-fire carbon found in LI stands (4388 +/- 235 g C m^{-2}) and 50% of the pre-fire carbon reconstructed for LI stands (5287 +/- 268 g C m^{-2}). For comparison, LI_{2005} stands stored 83% of the carbon found in their pre-fire reconstruction. Shallower post-fire SOH (H=67.7, df=2, p<0.001; Figure 5-3) and the virtual absence of wood biomass in the SI stands (Table 5-3) provide evidence for substantial consumption and loss of carbon stores from both soil and tree canopy layers in SI stands following two closely timed fires.

Depth of thaw did not differ between LI_{2005} and SI stands (F=1.3, df=1, p=0.21; Table 5-2), although both were deeper than in MF stands (F=58.0, df=1, p<0.001, and F=20.0, df=1, p=0.001, respectively). The absence of a detectable difference in depth of thaw between LI_{2005} and SI stands may be due to field measurement constraints, as the thaw was often deeper than the length of the probe in LI and SI stands (26 and 29% of measurements, respectively).

5.4 DISCUSSION

Stands that experienced a short fire return interval showed marked decreases in carbon stores, even when compared to stands burned in the same fire following a long fire return interval. While the proportion of carbon consumed in each fire was comparable in LI stands burned in 1990/91 and 2005, it was the additive loss of carbon over two consecutive fires that

resulted in a much greater reduction in carbon stores in SI stands. Although there has been a qualitative understanding that closely timed fires will result in additive carbon loss, this pattern has been quantitatively verified by this study.

Mature black spruce stands that burned with the more typical, longer fire return interval showed a smaller direct effect of fire on carbon stores, as the low severity fire left soil and canopy biomass pools largely intact. Estimates of carbon accumulation from this study are lower than carbon estimates predicted by accumulation curves for black spruce forests in interior Alaska (9700gC m^{-2}; Kane & Vogel, 2009), likely due to the more northerly and marginal location of the study area. The proportion of forest floor consumed in LI stands (62%) is comparable to similar stand types across Canada (36-72%; De Groot *et al.*, 2009). Stands that experienced a short fire return interval deviate from the trend, with 91% of the forest floor consumed over the two fires. These results indicate that variations in different aspects of the fire regime, such as frequency, can dramatically influence the magnitude of direct effects of fire on net ecosystem productivity and carbon storage.

The additive loss of carbon following repeat fires is intuitive; whether or not younger stands are likely to burn is less obvious. Younger stands may not have the biomass accumulation or structure to sustain a fire. In the case of this study, the biomass remaining from the previous burn was enough to sustain the fire in young stands. Although older stands are more flammable than younger stands (Schimmel & Granström, 1997), weather and local moisture conditions largely drive fire patterns in the boreal forest (Bessie & Johnson, 1995; Podur & Martell, 2009). Fire boundaries are also related to weather and edaphic conditions (McIntire, 2004). A fire may be less likely to ignite in young forests (Krawchuk *et al.*, 2006), but if it is already burning in an older stand and weather conditions are favourable, it may cross historic burn edges. Fire severity,

or biomass consumption, in younger and older stands is also highly related to weather (Renkin & Despain, 1992). In this study, the short-interval fire was severe enough to combust dead wood, live seedlings, and an equivalent proportion of SOH as was consumed in adjacent mature stands. Thus, the conditions in the short-interval burn prior to the 2005 fire did not appear to be a limitation on fire severity.

Previous research suggests that the loss of carbon via the removal of the organic horizons may initiate a positive feedback cycle that destabilizes the soil thermal regime (McGuire *et al.*, 2006; Schuur *et al.*, 2008). The organic horizons act as an insulating layer to the mineral soils, which helps maintain the permafrost table. Removing the organic horizons can result in increased soil temperatures and, in turn, a deepening of the active layer. Permafrost soils contain high carbon densities and store a large amount of the global carbon stocks (Davidson & Janssens, 2006; Schuur *et al.*, 2008). Permafrost thawing, or thermokarst, makes long-term (or deep) carbon stores in the permanently frozen soil available for decomposition (Schuur et al., 2009). This may be of greater concern than the direct loss of carbon by fire, as there is more carbon sequestered in permafrost soil than above in soil and canopy layers (Davidson & Janssens, 2006; Schuur *et al.*, 2008). Total soil carbon stored in the northern circumpolar permafrost zone has recently been calculated as at least 1672 petagrams (1 petagram = 1 billion metric tons; Schuur et al., 2008), and the release of a portion of that carbon from thawing permafrost will contribute a significant input into the atmosphere over the next century, potentially contributing to further permafrost melting (Schuur *et al.*, 2008; Schuur *et al.*, 2009; Tarnocai *et al.*, 2009). Thus, increases in fire frequency are likely to have effects on carbon cycling both directly through greater total carbon emissions from fire (per unit time) and indirectly through changes in the soil thermal regime caused by reduced organic horizon thickness.

Shortening the fire return interval has not only reduced the amount of carbon stored in these northern treeline forests, it has potentially altered the successional trajectory of these black spruce stands (Payette *et al*., 2001; Johnstone & Chapin, 2006a; Johnstone *et al*., 2010b). The complete removal of the black spruce aerial seed bank combined with the incineration of the seedlings established following the 1990-91 fires means that stand self-replacement is unlikely. I have shown that the organic horizon diminishes with a shortened fire return interval, which may favour light-seeded tree regeneration (Johnstone *et al*., 2010b). Although the successional trajectory of the short-interval burn is currently unknown, the probable ecosystem shift away from coniferous forest to a herbaceous or deciduous ecosystem (Johnstone & Chapin, 2006b) will have a significant impact on ecosystem functions potentially including increased albedo, decreased carbon storage, and further altered disturbance regimes (Chapin *et al.*, 2000; Eugster *et al.*, 2000; Chapin *et al.*, 2005; McGuire *et al.*, 2006).

The results of this study highlight the importance of including disturbance in calculations of net ecosystem carbon balance, which represents the carbon balance from all physical, biological, and anthropogenic sources and sinks (Chapin et al., 2006). Large losses in soil carbon due to fire consumption of the organic horizon can take a long time to reaccumulate, perhaps longer than the mean fire return interval. Both theoretical models (e.g., Kasischke et al., 1995) and empirical studies have shown that carbon storage in ground layers decreases with shorter fire return intervals. Lake islands with boreal forest cover in Sweden have been shown to have a negative association between long-term carbon accumulation and fire frequency (Wardle et al., 2003). More frequently burned larger islands accumulated less soil carbon per unit area than smaller islands with longer fire return intervals. In black spruce forests of eastern Canada, forest floor accumulation after a high severity fire can lag several decades behind accumulation after a

low severity fire (measured as biomass consumption; Lecomte et al., 2006). Black spruce stands that develop following a high severity fire, which results in biomass consumption comparable to that following a short fire return interval, can accumulate biomass for more than 700 years (Lecomte et al., 2006). Given the typical fire return interval of the northern Yukon study region, it is unlikely that short-interval burned areas will reaccumulate the biomass present prior to the fire before they burn again. While I do not expect that a 15-year fire return interval could be sustained in this ecosystem, the increased loss of carbon following a single short-interval fire has dramatically decreased the net ecosystem production of these northern forests, thereby reducing their role as a carbon sink.

5.4.1 Conclusions

More research is needed to quantify the effects of predicted increases in fire frequency (Westerling *et al.*, 2006; Wittenberg *et al.*, 2007; Turner, 2010). Here we used overlapping historic wildfires as a natural experiment or case study to examine the impacts of short disturbance intervals on ecosystem carbon stores. Because fire is a patchy, landscape process, studies of this type are likely to be inherently confounded with other spatial gradients. Nevertheless, given the practical impossibility of experimentally manipulating multiple, landscape-scale fires, case studies such as this one are likely to provide the best empirical data available on the potential impacts of altered fire regimes (Turner *et al.*, 1997). Here I have attempted to minimize spatial biases by selecting study sites with comparable pre-fire conditions and fire severity that were exposed to different fire return intervals caused by overlapping, natural wildfires. The results of this study provide some of the first empirical evidence for negative effects of increased fire frequency on carbon storage and net ecosystem productivity in boreal forests. Future research should aim to verify and expand these results through additional

studies of overlapping disturbances, particularly in the southern boreal zone, where stands recover more quickly following disturbance and resilience to disturbance may be different than sub-arctic stands. My observations of a shortened fire return interval leading to a change in the carbon storage capacity are consistent with output from ecosystem models that simulate changes in fire regimes (e.g., Kasischke *et al.*, 1995; Kurz *et al.*, 2008). Further comparisons between empirical data such as presented here and predictions from process-based models will be critical to improving our ability to forecast future ecosystem responses to ongoing changes in climate and fire regime (Flannigan *et al.*, 2009).

6.0 CONCLUSIONS

The boreal forest is a globally important biome, due in part to its large contribution to climate-ecosystem feedbacks (Bonan *et al.*, 1992; Chapin *et al.*, 2000; Chapin *et al.*, 2005) and its historic role as a net accumulator of carbon (Kasischke, 2000; McGuire *et al.*, 2002; Tarnocai *et al.*, 2009). Recent literature has called for the 'urgent' preservation of the boreal forest (Bradshaw *et al.*, 2009), in part because of its important role in terrestrial carbon storage.

Climate is changing, particularly in the circumpolar north where summer air temperatures are increasing (Chapin *et al.*, 2005). Warming temperatures can have many effects on arctic ecosystems. In addition to responses such as increased vegetation growth and distribution (Epstein *et al.*, 2000; Jia *et al.*, 2003), it is also anticipate that historic disturbance regimes will change. Fires are expected to burn larger areas of the boreal forest and occur more often (Kasischke & Turetsky, 2006; Balshi *et al.*, 2009; Flannigan *et al.*, 2009). The number of individual fire events, number of large fires, and area burned have increased across Canada and Alaska since the 1960s (Kasischke & Turetsky, 2006). The interaction between climate warming and the fire regime and their effect on successional processes in the boreal forest is largely unknown. Recent research in Alaskan boreal forests suggests that warming temperatures have weakened the resilience, i.e., the ability to recover quickly after perturbation, of the boreal forest to the increasing frequency of disturbance (Chapin *et al.*, 2010). The possible ecosystem shift away from coniferous forest to a herbaceous or deciduous ecosystems with more frequent disturbance (Johnstone & Chapin, 2006b; Chapin *et al.*, 2010) will have significant impacts on ecosystem functions including increasing albedo, decreasing carbon storage, and altering future disturbance regimes (Chapin *et al.*, 2000; Eugster *et al.*, 2000; Chapin *et al.*, 2005; McGuire *et al.*, 2006).

The goal of this research was to investigate the interaction between fire and forest successional processes in sub-arctic boreal forest stands undergoing climatic warming (Chapin *et al.*, 2005; Figure 1-1). The research summarized here contributes to our understanding of how climate warming, disturbance regimes, and vegetation may interact, resulting in secondary successional pathways that differ from historic patterns. This research has resulted in four main conclusions regarding these interactions: 1) northern forest stands are an important seed source for treeline expansion; 2) short fire return intervals interrupt the serotinous strategy of stand self replacement after fire; 3) fire stimulates periods of regeneration in the boreal forest, and the length of the fire return interval affects the composition and suitability of the seedbed for post-fire recruitment; and 4) carbon storage capacity across disturbance intervals is dramatically reduced following short interval burns. Here, those main conclusions are synthesized to examine broader implications for stand dynamics under a changing fire regime in sub-arctic boreal forests.

6.1 Northern forest stands as a seed source for treeline expansion

I identified a gradient of reproductive potential across the treeline ecotone in sub-arctic black spruce stands in northern Yukon (Chapter 2). Seed production and viability were low in transitional, open forest, and treed tundra stands, leaving northern forest stands to fill the role of seed source for black spruce range expansion. The structure of and processes within northern forest stands therefore influence the potential for future range expansion. This pattern has also been observed in sub-arctic boreal forest in Québec, where current treeline position reflects past climatic conditions (Payette *et al.*, 2001). In the eastern boreal forest stands, current reproductive output was minimal at the forest-tundra transition. The current limit of tree occurrence is hypothesized to occur beyond the boundary where climate favours sexual reproduction, thus

sexual reproduction is dependent on more southern stands. In altitudinal treelines near the northern limit of black spruce's range in Alaska, reproduction of black spruce was predominately clonal three decades after fire due to low seed production and viability (Lloyd *et al.*, 2005), further stressing the importance of northern forest stands as a seed source for black spruce range limits. The results presented in this thesis provide insight into the potential for change in forest structure near in northern Yukon.

Although I identified a source of viable seed in the black spruce treeline ecotone, seed availability is not the only requirement for range expansion. There must also be a suitable seedbed for recruitment, which, in the northwestern boreal forest, often requires fire to reduce competition and release nutrients for successful seedling establishment (Johnson, 1992; Payette, 1992). We have a broad understanding of the recruitment requirements for stand self-replacement in the boreal forest. We do not yet know how post-fire conditions will differ with warming temperatures, and how dominant northern boreal species, such as black spruce, will respond. Further understanding the recruitment requirements of northern boreal stands will provide a mechanistic understanding of the impacts of disturbance on the composition and dynamics of these boreal forests.

6.2 Post-fire regeneration in black spruce forests

This research has led to a greater understanding of the mechanisms driving post-fire stand self replacement in northern black spruce forests (Chapter 3). Reproductively mature black spruce stands release viable seed onto the seedbed during each growing season. Seedlings rarely becomes established on the mature forest floor due to poor seedbed quality. However, once the forest floor has burned, the number of safe seed sites for black spruce establishment increases dramatically. Black spruce seed is released from semi-serotinous cones and many individuals

establish in the first few years following a fire. Black spruce seedlings establish best in moist microhabitats, and in northern stands underlain by continuous permafrost, those microhabitats occur in hollows between earth hummocks. The pairing of post-fire seed release and increased seedbed availability is key to post-fire self replacement. The suitability of the seedbed for black spruce recruitment decreases with time since fire, leaving a short window of opportunity for stand establishment.

6.3 Short fire return interval interrupts serotiny

Experimental research summarized in this thesis revealed constraints on secondary succession after short-interval fire in northern black spruce stands. Overwhelmingly, the biggest constraint on post-fire stand self replacement was the lack of seed after a short-interval fire (Chapter 3). Black spruce takes several decades to mature in northern forest stands (Black & Bliss, 1980; Morneau & Payette, 1989; Viglas, 2011) and the 2005 fire occurred well before there was adequate seed on-site for self replacement. The results presented in this thesis provide strong empirical evidence that disturbance, although essential for stand renewal, may limit forest recovery or expansion when the supply of viable seed is low.

Lack of seed was also cited as the cause of regeneration failure after fire in upland black spruce stands in the forest-tundra transition in sub-arctic Québec (Sirois & Payette, 1989). The reason for low seed availability in the eastern sub-arctic stands differed from that of the research summarized in this thesis. In northwestern boreal stands, black spruce seed was lacking due to an interruption to the serotinous strategy, caused by two closely timed fires. In the forest-tundra transition of Québec, the lack of seed was due to scant sexual reproduction of individuals that burned (Sirois & Payette, 1989). As described above, the current location of the black spruce treeline in sub-arctic Québec is beyond the limit of favourable environmental conditions for

sexual reproduction (Payette *et al.*, 2001). Although these stands likely initiated during fire, declining climatic conditions since their establishment led to reduced production of seed. Their persistence is the result of clonal reproduction and low fire frequency (Payette *et al.*, 1989; Sirois & Payette, 1989). The outcome of the regeneration failure differs markedly in the two regions, as well. In contrast to the grass-dominated tundra present in the first few years after fire in my western boreal study area, black spruce regeneration failure resulted in sub-arctic Québec resulted in a shift to typical sub-arctic lichen and shrub tundra (Sirois & Payette, 1989; Payette *et al.*, 2001). Both the Yukon (research presented in this thesis) and Québec studies implicate post-fire seed availability as a potentially critical bottleneck in disrupting the regeneration of these forests.

6.4 Seedbed characteristics

Seedbed condition was the second major constraint to secondary succession observed through field experimentation summarized in this thesis. Seedling emergence of black spruce observed in this study is a good example to illustrate successional constraints by substrate on recruitment. Black spruce seedlings emerged well in long-interval burned stands, both on earth hummocks and hollows (Chapters 3 and 4). Seedling emergence increased when seed was artificially added to long-interval burned stands. Mature forest stands received the same amount of naturally dispersed black spruce seed as long-interval burned stands. However, even after increasing the amount of black spruce seed by artificial seeding, there was very little recruitment in mature forest stands. Seedbed, not seed availability, therefore constrained black spruce recruitment in mature forests. Once mature forest seedbeds have become established, disturbance is required to initiate new phases of sexual regeneration. These responses reinforce the long-term impact of a recruitment failure after fire.

Reduced black spruce emergence in short-interval burned stands indicated that seed availability was the major constraint on post-fire recruitment. The number of black spruce that emerged in short-interval burned stands was less than long-interval burned stands, particularly on earth hummocks. This suggests that the seedbed in short-interval burned stands was less suitable for black spruce emergence than that of long-interval burned stands. The patterns observed in microtopographic environmental conditions led to the conclusion that limited seedbed moisture constrained black spruce emergence after short-interval fire (Chapter 4). Black spruce seedlings are highly sensitive to moisture stress (Black & Bliss, 1980; Thomas & Wein, 1985). Thus, seedbed condition reduced black spruce emergence in mature forest and short-interval burned stands, albeit for different reasons and with a different magnitude of effect.

The final component of seedbed constraints on post-fire regeneration is related to the age of the burned stand. Post-fire seedbeds provide a short window of opportunity for tree recruitment that can then remain closed until the next fire. With time since fire, the amount of available seedbed for tree establishment decreases. Previous research has shown recruitment pulses of conifers associated with seedbed availability after disturbance (Johnson & Fryer, 1989; Sirois & Payette, 1989; Johnstone *et al.*, 2004; Lloyd *et al.*, 2005; Peters *et al.*, 2005), where the majority of individuals establish within the first decade after fire. After a historically typical, long fire return interval, moss, bryophyte, and lichen species also begin to colonize a stand in the first few years after fire. Within two to three decades after fire, these species have established enough to create unsuitable seedbed for trees (Kershaw, 1977; Payette *et al.*, 1985; Morneau & Payette, 1989). If a spruce seed is able to germinate on this type of surface, it is likely to die due to desiccation (Charron & Greene, 2002; Jayen *et al.*, 2006). This thesis presents empirical

evidence of scant seedling emergence on moss and lichen seedbeds in mature forest stands (Chapters 3 and 4).

The amount of suitable seedbed also decreases with time since fire in short-interval burned stands, as well. In the study area, stands were dominated by reed-grass (*Calamagrostis lapponica* (Wahlenb.) Hartm.) and other early successional herbaceous species (C.D. Brown, personal observation). Experimental work with *C. canadensis* (Michx.) P. Beauv. in Alaskan boreal sites showed that it had a strong inhibitory effect on spruce and birch seedling establishment, likely due to unfavourable temperature and moisture conditions created by the grass (Cater & Chapin, 2000). In the northern Yukon black spruce stands studied in this thesis, reed-grass and other herbaceous species created a very different seedbed than typical, post-fire succession in boreal forest stands. Over the first few years following fire, they formed a layer of dead plant material, or litter, creating a barrier to the surface of the soil organic horizon. This barrier became increasingly evident each field season of this study. Field observation of seeded tree seedlings became more difficult as reed-grass, horsetail (*Equisetum arvense* L.), and fireweed (*Epilobium angustifolium* L.) abundance, and thus litter, increased, which I compensated for by increasing seedling search time in those plots. The litter barrier further reduced the number of available sites for seed germination and seedling emergence.

These responses demonstrate the vulnerability of serotinous species to rapid and persistent shifts in stand dominance following two closely timed fires. Two steps are critical to ensure regeneration in these black spruce forests. First, the stand must have time to become reproductively mature and produce enough seed for self-replacement, and secondly, the seedbed must be suitable for recruitment after fire. In short-interval burned stands studied here, black spruce seed was not available and the seedbed for black spruce recruitment was less suitable than

in long-interval burned stands. The results presented in this thesis lead to the hypothesis that seedling emergence is more of a limiting step to post-fire recruitment than seedling growth and survival. Through experimentation, I showed that planted seedlings tended to survive and prosper in burned areas, even where seedlings were unable to emerge from seed. This further highlights the critical need for safe seed sites for successful tree recruitment after fire.

Although seedbeds in short-interval burns were less suitable for black spruce establishment than in long-interval burned stands, the lack of available seed was a much greater constraint on post-fire regeneration than seedbed availability (Chapter 3). If black spruce seeds were available in the first few years following short-interval fire, stand recovery would likely occur. However, the post-fire density of black spruce may be reduced following a short-interval fire, in comparison to recovery after a long-interval fire.

The research presented empirically demonstrates a failure in black spruce recruitment after fire. The stands studied were not near any other seed source that would allow colonization by another native boreal tree species after the second fire. However, not all northern black spruce stands are as monospecific as the one studied here. Thus, the potential for other species to colonize was investigated through experimental seeding and planting with the aim of identifying links between specific substrates and seedling emergence.

6.5 Potential colonizers of short-interval burned stands

Species-specific patterns in emergence, survival, and growth in the three fire history classes were identified through field experimentation (Chapter 4). Several observations from this study led to the conclusion that short-interval burned stands had drier and warmer soils than stands burned within the typical fire return interval. These soils were suitable for the emergence of Alaskan birch and white spruce seedlings. However, black spruce recruitment was associated

with greater moisture microhabitats, thus a decline in moisture associated with, for example, short-interval burns, reduced precipitation, or changes to the soil thermal regime may result in lower black spruce emergence and survival after fire. Thus, seedbed composition was less suitable for black spruce (although recruitment still occurred) but was suitable for typical upland species such as white spruce and Alaskan birch after a short fire return interval. Even with fire return intervals longer than we investigated here, we may find that moisture constraints reduce post-fire recruitment or shift stand dominance to alternate species (Johnstone *et al.*, 2010c), where seeds are available.

6.6 Implications: carbon storage

The consequences of a shift in secondary succession go beyond just a change in species composition. The results presented in this thesis provide some of the first empirical evidence for negative effects of increased fire frequency on carbon storage and net ecosystem productivity in boreal forests (Chapter 5). This study provides evidence that a shortened fire-return interval in the boreal forest increases net loss of soil carbon over a fixed period of time and reduces the residual organic horizon thickness of the post-fire forest. Thus, increases in fire frequency are likely to have effects on carbon cycling both directly through greater total carbon emissions from fire (per unit time) and indirectly through changes in the soil thermal regime caused by reduced organic horizon thickness.

Given the typical fire return interval of the northern Yukon study region, it is unlikely that short-interval burned areas will reaccumulate the biomass present prior to the fire before they burn again. While it is not expected that a 15-year fire return interval could be sustained in this ecosystem, the increased loss of carbon following a single short-interval fire has dramatically decreased the net ecosystem production of these northern forests, thereby reducing

their role as a carbon sink. Fire frequency has been cited as the driver behind variations in landscape carbon balance in the boreal forest systems of North America (Bond-Lamberty *et al.*, 2007), and increased carbon losses after short interval fires have been observed in boreal systems globally (e.g., Turetsky *et al.*, 2002; Wardle *et al.*, 2003; Lecomte *et al.*, 2006).

6.7 Indirect effects of climate change

With warming temperatures, it is expected that tree ranges will expand northwards as environmental constraints on growth and establishment lessen (Kaplan *et al.*, 2003; Holtmeier & Broll, 2005). Warming temperatures may allow fires to occur more often (Balshi *et al.*, 2009; Flannigan *et al.*, 2009). The research I summarize in this thesis provides empirical evidence of rapid vegetation change at the northern margin of the boreal forest due to a shortened fire return interval. These results lead me to hypothesize that the indirect effects of warming summer temperatures on the disturbance regime outweigh direct temperature effects. Instead of tree range expansion, I have documented the local degradation of treeline forests. As these stands act as a seed source for treelines, this degradation may have long-term consequences for tree range expansion into tundra ecosystems, and could potentially cause treeline recession or fragmentation. This provides further evidence that treeline response to climatic change is not as straightforward as northward range expansion (Harsch *et al.*, 2009; Harper *et al.*, 2011).

An interruption to the serotinous regeneration strategy of black spruce caused by the short fire return interval has changed the post-fire composition of the black spruce stands studied. Here, a shift from a cycle of black spruce stand self-replacement will likely persist for some time, not only due to the lack of seed for recruitment but also the loss of suitable seedbeds with time since fire. The absence of any seed source within dispersal distances (C. Brown, personal observation) means that the short-interval burned stands are unlikely to regenerate as

forest (Chapter 4). Even if a seed source became available in the near future, by then the seedbed would be unsuitable for recruitment. These results support the hypothesis that disturbance events can initiate shifts in forest cover in stands that are experiencing directional environmental change (Johnstone *et al.*, 2010a). An unusual fire event that occurs during a period of climatic warming, for example, can disrupt plant and soil feedbacks that contribute to stand resilience and facilitate stand-self replacement after fire, initiating a shift to a new successional trajectory (Frelich & Reich, 1999; Johnstone *et al.*, 2010a). In the research presented here, I have demonstrated that an unusual fire event in a region undergoing warming summer temperatures has caused a black spruce colonization failure, a reduction of the soil organic horizons, and an alteration of the seedbed characteristics, together disrupting black spruce regeneration after fire.

I predict that the short-interval burned stands studied here will remain grass- or shrub-tundra communities in the absence of tree recruitment. Currently, the short-interval burned stands are composed of *Calamagrostis* sp. grass-dominated communities. I observed patches of suitable seedbed for recruitment of artificially seeded Alaskan birch and white spruce in short-interval burned stands in the first few years after the 2005 fire. However, there were few individuals of tree species, such as Alaskan birch or white spruce, within dispersal distance of the short-interval burned areas. As time since fire increases, grass and other herbaceous plant litter will continue to accumulate, leaving increasingly fewer sites for tree seeds to successfully establish. Following extensive stand mortality of drought-stressed white-Sitka spruce (*Picea sitchensis* (Bong.) Carr. hybrids by insect infestation, forested stands in Alaska shifted to grass dominance by *Calamagrostis canadensis* (Berg *et al.*, 2006). As discussed above, the microenvironment created by *Calamagrostis* sp. can inhibit spruce and birch seedling establishment (Cater & Chapin, 2000).

The shift from black spruce forest stands with thick soil organic horizons to grass or shrub tundra has significant implications for ecosystem services such as carbon storage, permafrost degradation, and albedo. Thick soil organic horizons insulate permafrost layers, which sequester large quantities of carbon. Thinner organic horizons may cause permafrost warming, leading to the degradation of long-term carbon stores. These changes to the soil thermal regime may then cause further soil warming and changes to soil drainage, influencing future nutrient cycling (McGuire *et al.*, 2006; Schuur *et al.*, 2008; Schuur *et al.*, 2009). This ecosystem shift also has implications for wildlife habitat and human subsistence use. Currently, the mature black spruce stands in the northern Yukon study area support several species of edible berries and provide wintering grounds for the Porcupine caribou herd (Russell *et al.*, 1992), all of which are important subsistence foods for the Vuntut Gwitchin of Fort MacPherson, NWT.

The research presented here demonstrated that fire-induced effects on forest succession were in the opposite direction of what has been predicted for northern forest responses to climate. This is one example of an ecosystem shift following a change to the disturbance regime, presumably caused by changes to the climate. Recently, interruptions to historic successional trajectory have been observed in ecosystems globally, both in serotinous and non-serotinous plant systems (e.g., Chapter 3; Keeley *et al.*, 1999; Folke *et al.*, 2004; Jasinski & Payette, 2005; Johnstone & Chapin, 2006b; Frelich & Reich, 2010). The vegetation of the boreal forest is thought to have been resilient to climatic change in the past, due in part to the adaptations that conifers have for post-fire regeneration (Chapin *et al.*, 2010). What this thesis and other studies have documented are the consequences or outcomes of the indirect effects of climate. Specifically, here I have highlighted the vulnerability of boreal forest communities to disturbance events that are outside the historic disturbance regime. The results presented here are

applicable to disturbance-driven communities across the boreal forest of North America. While upland black spruce sites were studied in this thesis, the responses documented here are relevant to lowland forests in the region, as well as serotinous boreal forests in Alaska, which undergo similar dynamics to the study forests. This research is also relevant to eastern boreal forests of North America. As discussed earlier, the cause of black spruce recruitment failure after fire in Québec sub-arctic stands is different than those studied here. However, the research presented in this thesis further increases our understanding of the mechanisms behind an interruption in secondary succession in black spruce forests. With climate change, altered disturbance regimes and unusual disturbance events are increasing (Turner, 2010). We need to further our understanding of the processes that control ecosystem dynamics under current conditions, and how those processes may be interrupted, leading to compositional change in the future.

6.8 Future research

We still have much to learn about the complex interactions between climate, fire regimes, and vegetation in boreal forest ecosystems. Future research should include more empirical studies of ecosystem changes under novel disturbance regimes. Additional research should also focus on the mechanisms underlying boreal forest structure and function in northern ecosystems, which are already experiencing climatic change. Such studies, in combination with the research presented in this thesis, will aid in our management of boreal forest stands and will help us to predict and prepare for the outcomes of climate change.

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8.0 APPENDIX A: SITE-LEVEL STAND DATA

Table A1: Site-level characteristics of study sites in the North Yukon.

Fire history	Site	Stand density (trees/ha)	Basal area (m^2/ha)	Depth of thaw (cm)	Soil organic horizon thickness (cm)	
					Hummock	Hollow
Mature forest	1	6167	11.4	37.6	11.2	12.4
	2	4167	5.7	33.4	14.6	19.6
	3	3333	5.7	37.5	12.5	16.8
	4	2833	6.6	37.7	13.4	17.0
	5	5833	11.4	36.5	5.4	10.2
	6	5000	6	38.2	7.9	5.7
	7	6000	12.2	58.6	7.8	1.5
	8	3333	4.5	42.6	10.7	5.1
Long-interval burn	1	5667	10.5	62.6	12.4	11.2
	2	7667	10.4	89.7	19.6	14.6
	3	6500	15.5	84.3	16.8	12.5
	4	5333	23.8	79.1	17.0	13.4
	5	3833	13	101.1	10.2	15.4
	6	2667	9.8	65.1	5.7	7.9
	7	4500	15.5	82.1	1.5	7.8
	8	1667	5.5	79.3	5.1	10.7
Short-interval burn	1	-	-	91.3	1.8	2.3
	2	-	-	n/a	0	0.7
	3	-	-	79.2	0.7	1
	4	-	-	65.5	6.8	0
	5	-	-	78.4	4.3	0.7
	6	-	-	52	0	0
	7	-	-	94.6	3	0.8
	8	-	-	93.5	3	1.3